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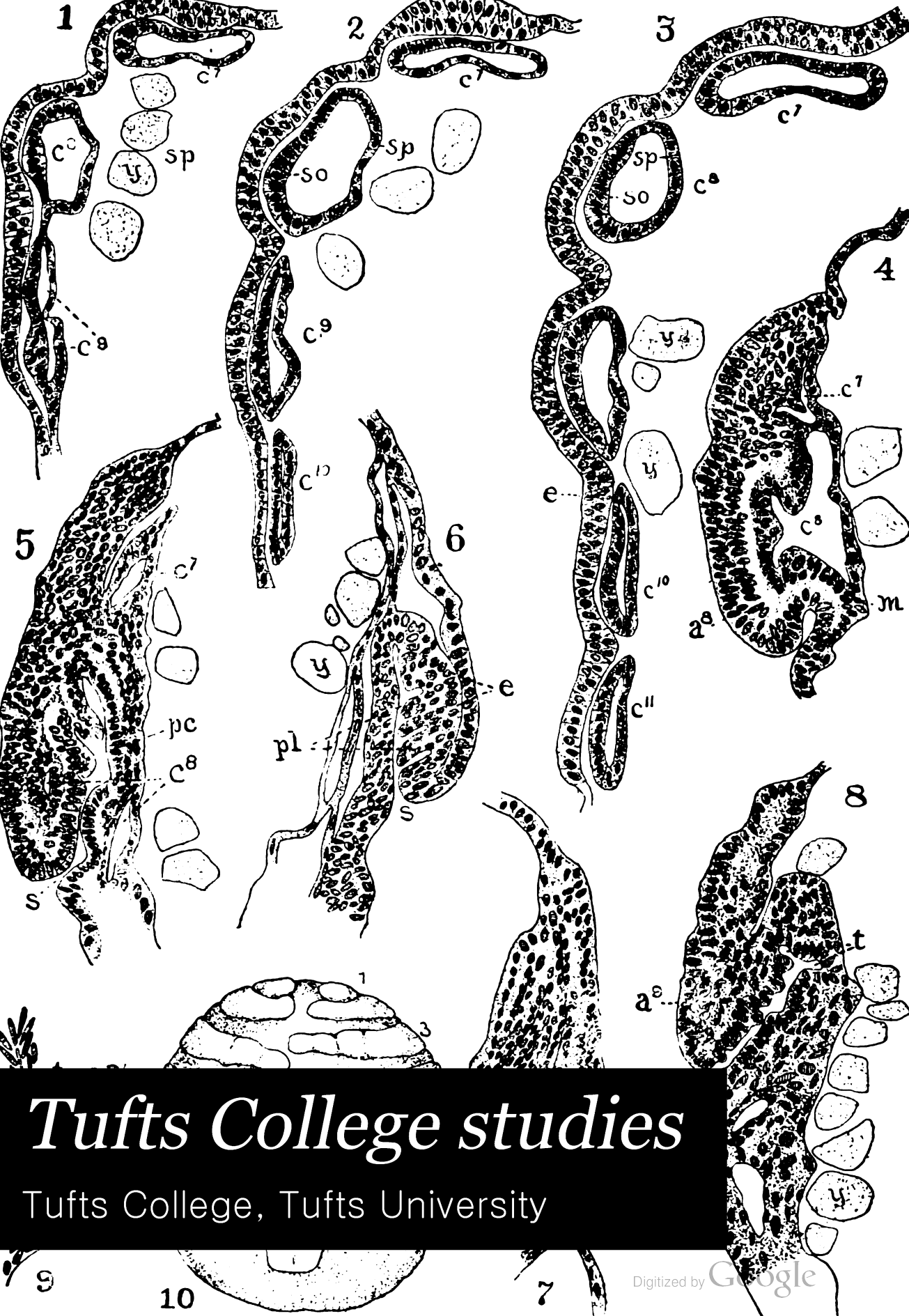

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TUFTS COLLEGE STUDIES, NO. I.

MUSEUM OF COMPARATIVE ZOOLOGY CAMBRIDGE, MASS.

THE ANTERIOR CRANIAL NERVES OF PIPA. By G. A. Arnold.

ECTODERMIC ORIGIN OF THE CARTILAGES OF THE HEAD. By Julia B. Platt.

THE CLASSIFICATION OF THE ARTHROPODA. By J. S. Kingsley.

TUFTS COLLEGE, MASS.
March, 1894.

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TUFTS COLLEGE STUDIES, NO. I.

THE ANTERIOR CRANIAL NERVES OF PIPA AMERICANA.[1]

By G. A. Arnold.

This study was undertaken to extend the method of serial sections so successfully employed by Von Plessin and Rabinowicz ('91) on *Salamandra maculata*, to one of the Anura. The embryos of Pipa, which form the basis of the study, had a body length of 9 mm. and were cut transversely into sections 22½ micra thick, stained with alum cochineal and Bleu de Lyon (the latter after Röse's method ('91), and the reconstructions were made by plotting the projections of the sections on cross-section paper. It is only by such methods that detailed and conclusive knowledge can be obtained of the distribution of the nerves in the smaller forms. Since this method has been used in so few instances, comparison with other Batrachia is impossible, and so the text is solely descriptive. It is, in fact, but an extended explanation of the plate to which reference must be made for all details. In my account of the several nerves, I have omitted detail with regard to such features as are common to all Batrachia, and have dwelt more especially upon points previously unknown or apparently peculiar to this form. So far as I am aware, the nervous system of Pipa has been studied previously only by J. G. Fischer, whose paper, unfortunately, is not to be found in the libraries I have consulted.[2]

[1] Reprinted from the "Bulletin of the Essex Institute," Vol. XXVI, pp 1-9, 1893.

[2] Since this article left Mr. Arnold's hands, I have been able to consult Fischer's account of Pipa ('43), and find his description of the adult to vary widely from the young, as may be seen by comparing the adjacent outlines of Fischer's figure. The differences are great and important, and in most respects I feel confident that Mr. Arnold's account is correct. This is especially the case with regard to the origins of nerves V–VIII. In Fischer's figure there are two roots for these nerves, and the VIII is connected to the V–VII by a ramus communicans. In the young I am positive,

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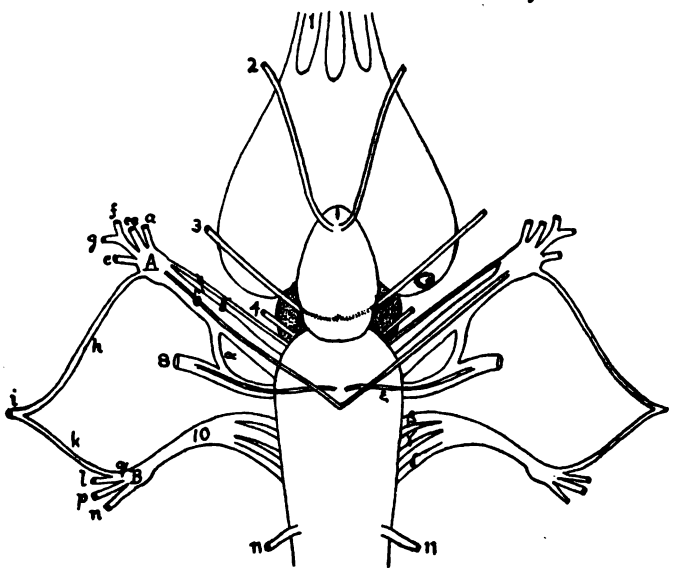
VIII (Auditory) VII (Facial) and V (Trigeminal) nerves.—These three nerves have a common origin from the side of the medulla oblongata, arising by fibres among which the roots of separate nerves cannot be distinguished.

that such conditions do not exist. Careful study of both sides of two series of sections shows no interruption of the cerebral membranes between the Gasserian ganglion and the common origin of V–VIII. In the method of origin of the nerves from the Gasserian ganglion, again, similar differences may be seen. To compare them in detail would be simply a duplication of the accounts of Fischer and Arnold, and so the reader is left to compare the figures for himself. These differences cannot be regarded as due to different stages of growth, but are easier explained as arising from the different methods of work.

J. S. KINGSLEY.



Outline reproduction of Fischer's figure ('43) of the brain and cerebral nerves of *Pipa americana.* "Fig. 1. Pipae dorsigerae nervi cerebralis, 1–4; Parium quattuor priorum radices. 5; Radix magna (sensitiva?) Trigemini.—η: Radix minor (motoria?) Trigemini.—6: Abducens cum ganglio Trigemini coalescens.—α: Radix ab Acustico in Trigeminum immissa.—A: Ganglion—a: ramus nasalis.—e: R. maxillaris inferior.—ee: R. maxillaris superior.—f. R. palatinus.—g. R. mentalis (alveolaris Salamandrinorum).—h: R. ingularis.—8: Acusticus.—ε: Radix ipsius minor inferior (Facialis?).—μ: radix superior. —10: Vagus β, γ, δ Tres ipsius radices, quarum γ et δ duabus iterum minoribus componuntur. B: Ganglion vagi.—9: Glossopharyngeus.—h: Ramus communicans.—l R: lingualis.—n R. intestinalis.—p. R: cutaneus.—11: Accessorius Willsii."

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The auditory nerve separates directly and goes to the large auditory ganglion, situated in a foramen in the wall of the otic capsule immediately opposite the common origin of the three nerves from the medulla.

From this ganglion three groups of nerves arise, which may be taken up in order, beginning with the most posterior. The posterior ramus or group consists of the ramulus posterior (*r. p.*) the ramulus neglectus (*r.a.neg.*), the ramulus basilaris (*r.bas.*), and the ramulus lagenæ (*r.a.lag.*). The ramulus posterior leaves the posterior side of the ganglion, and runs outward and backward to the ampulla of the posterior semicircular canal, over the sensory epithelium of which it is distributed. The ramulus neglectus leaves the ganglion in company with the preceding nerve and soon distributes itself to the pars neglecta of the sacculus. The ramulus basilaris has a similar course to the pars basilaris of the cochlea. The fourth and last of this group, the ramulus lagenæ, has a more ventral origin, and runs somewhat ventrally to the lagena. The second branch of the auditory nerve, the ramulus sacculi, consists of a large branch running outward and spreading slightly, forming a large brush distributed over the macula acustica on the lower side of the sacculus. The third group consists of the nerves to the two anterior ampullæ. They arise as a single nerve from the anterior side of the ganglion and run forward and outward. Then they divide to go to their respective ampullæ. The ramulus anterior (*r.a.a.*) makes a turn around the external semicircular canal to reach its own ampullæ.

After the separation of the auditory nerve, the V and VII continue forward along the side of the brain, until they enlarge into a ganglion—the Gasserian—oval as viewed from above, situated proximally within and distally without the cranial walls. The facial nerve arises as two branches, one lateral, the other ventral, near the middle of this ganglion. The former of these (*coms.g.*) forms the commissure between the facial nerve and the glossopharyngeal. Its course is at first outward, then it curves backward in an horizontal plane until it joins the glossopharyngeal nerve directly opposite the origin of the V, VII and VIII from the brain. Its further

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course is that of the glossopharyngeal. The large loop which it forms is necessitated by the fact that it has to pass around the otic capsule, close to the walls of which it runs.

The other branch, the facial proper (*fac.*) takes an outward and downward course from its origin from the ventral side of the ganglion. It soon divides into a large ramus to the lower jaw (*hy.man.*) and a palatine ramus (*p.*), to the roof of the mouth. Immediately on separation the palatine runs forward and inward and then directly forward above the roof of the mouth, until near the anterior wall of the orbit it gives rise to an anastomosing commissure connecting it with the ramus nasalis of the trigeminal. Beyond this commissure the palatine bends inward and distributes itself to the epithelium of the mouth and the internal choana. I do not find a branch of the palatine continuing forward through the vomer to the region of the snout as in other Batrachia. The fact that the nerve does not extend forward to the nose precludes the possibility of there being any connection between it and the frontalis or nasalis other than the commissure above mentioned. A terminal connection between the palatine and the trigeminal is described by Ecker in *Rana esculenta.* He also mentions a double origin for the palatine from the separate ganglions of V and VII. My study of Pipa gives no indication of such a dual condition, since the nerve arises not from the common ganglion of the V and VII, but as a branch of the facial nerve.

After the separation of the palatine, the main branch of the facial (*hy.man.*)[3] turns outward and backward for some distance, passing along a groove in the ventral side of the otic capsule, between it and the roof the mouth. Thence it passes downward around the buccal cleft to the lower jaw. After making this turn, the hyomandibularis runs forward on the inner side of Meckel's cartilage along the floor of the mouth. It soon gives off a branch (*buc.*), which, in turn, divides to innervate the mucous lining of the mouth. This branch, although scarcely larger than several that are given off later as terminal branches with similar distribution, corresponds

[3] Hyomandibularis, von Plessin = Jugularis, Fischer = Facial, Wyman.

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most nearly to the buccalis of other forms. The main nerve continues its course forward, following the general contour of the jaw and is distributed to the inner lining of the mouth. The chief points of interest in connection with the facial in Pipa are the relations of the palatine and the apparent lack of connection between the facial-glossopharyngeal commissure and the facial proper. This of course is to be explained by the peculiar relations of the VII to the V, the facial first appearing as a distinct nerve coming from the trigeminal ganglion, the connection existing in the ganglion itself.

The trigeminal nerve consists of three divisions arising by as many separate roots from the anterior end of the Gasserian ganglion. These three divisions will be described in order corresponding to their origin from the ganglion, namely, the mandibularis, the frontalis, and the supramaxillaris superior.

The mandibularis (*man.*)[4] arises from the dorsal side of the anterior end of the Gasserian ganglion and runs outward, upward and forward. Then it turns in a gradual curve backward and in a sharp curve downward through the masseter and temporal muscles until it reaches the angle of the lower jaw, along the outer side of which it runs forward. Just outside of the Gasserian ganglion the mandibularis gives rise to a branch (*mas.*) which innervates the masseter and temporal muscles. Soon after entering the lower jaw it divides into the mandibularis proper and the mentalis which have their usual distribution. The mentalis has at first a more outward course, but later passes inward under the mandibularis to be distributed to the outer skin of the lower jaw. The mandibularis follows along the outer side of the mandible until it almost reaches the symphysis menti, to the integument of which region it is distributed. The only feature especially worthy of notice is that this nerve arises directly from the ganglion, not as a branch of the maxillaris superior.

The frontalis (*f.*)[5] arises beside the mandibularis, in juxtaposition with which it runs at first and preserves a slightly dorsal and lateral direction forward, passing over the masseter

[4] Mandibularis, Von Plessin and Rabinowicz=Maxillaris inferior, Fischer=Lower jaw branch, Wyman.

[5] Frontalis, Von Plessin and Rabinowicz=Nasalis, Fischer=Ophthalmic, Wyman.

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and temporal muscles to reach the orbit. Here it is deflected downward and inward around the eyeball. Then it ascends again upon the anterior side of the orbit and branches outward to innervate the skin of the cheek and the side of the upper jaw. This distribution differs from that in the common frog, where the frontalis sends branches to the lining of the nasal capsule, thus making terminal connection with fibres of the olfactory, and also where the frontalis pierces the premaxillary bone and exchanges fibres with the palatine nerve. This region of the snout is entirely supplied by the maxillaris and nasalis in this form. I failed to discover any branch to the muscles of the eye.

The supramaxillaris superior[6] is the largest ramus of the trigeminal. Almost immediately after leaving the Gasserian ganglion, from the anterior end of which it takes its origin, it becomes divided into two branches: 1. The maxillaris proper; 2. The nasalis of Von Plessin and Rabinowicz.

These two branches have a similar course forward, turning slightly inward and downward. The maxillaris takes a more ventral course than the nasalis, although they do not become widely separated until after the anastomosis between the maxillaris and the palatine has occurred. The maxillaris and the palatine run very nearly parallel throughout their courses and at no very great distance from one another; hence the commissure between them is short compared with its length in most Batrachia. It also presents another and more marked difference from the conditions obtaining in most Batrachia, in that its course is vertical rather than horizontal. After this anastomosis has occurred, the maxillaris continues forward in two branches which distribute themselves in the region of the nose and the side of the jaw. No terminal filaments connecting this nerve with the frontalis or the palatine can be traced.

The nasalis[7] (*n.*) lies slightly above the maxillaris after their separation, and so preserves an almost horizontal course forward to the tip of the nose, in which region one of its branches

[6] Supramaxillaris superior, Von Plessin and Rabinowicz=Supramaxillaris, Ecker =Upper maxillary branch, Wyman=Maxillaris superior, Fischer.

[7] Nasalis, Von Plessin and Rabinowicz.

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(*a*) is distributed. Branch (*b*) of the nasalis branches outwardly and distributes itself to the integument of the side of the upper jaw. Shortly after the nasalis has divided from the maxillaris, a large branch (*c*) splits off with the following course and distribution: The nerve turns sharply inward and passes over the olfactory nerve to which it gives off a small branch. Thence its course is downward and forward near the roof of the mouth to the snout, passing downward through the premaxillary bone for distribution to the region of the upper lip.

There arises from the supramaxillaris superior soon after leaving the Gasserian ganglion, a nerve which follows along near its parent until it reaches the orbit in which it bends upward and outward. Then it leaves the orbit and turns upward, backward and inward, distributing itself to the cutaneous layer on the top of the head midway between the eyes. This nerve is apparently the same as that which Fischer has described in the case of Necturus, as innervating the skin of the dorsal surface of the head. According to Huxley (Encyl. Brit., Art. Amphibia), it occurs only in the tadpole of Anura and disappears from the adult.

From the maxillaris superior, there also arises a nerve which innervates the superior oblique eye muscle, and hence is to be regarded as the trochlearis which has remained fused with the fifth, a condition possessing much morphological interest.

The oculomotor nerve (*o.c.m.*) arises the ventral side of the medulla oblongata. Its course is outward and forward within the chondrocranium, then it leaves the chondrocranium through the same foramen as the trigeminal and runs forward to be distributed in the usual manner to the rectus muscles of the eye. The only feature worthy of comment is the absence of a separate foramen for its exit from the cranium.

The optic nerve (*op.*) presents no special features, either in regard to its origin or its course. Its roots form a very intricate chiasma.

The olfactory nerve (*ol*) arises from the anterior extremity of the olfactory lobe, passes out through the walls of the skull, and distributes itself to the epithelium of the nasal capsule and

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to the organ of Jacobson in two branches. There is no indication of two roots like those described by Wiedersheim in the Gymnophiona, and which have later been commented upon by Burckhardt.

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EXPLANATION OF PLATE.

(REFERENCE LETTERS.)

a. b. c. = terminal branches of nasalis.
buc = buccalis.
com.g. = commissure of VII and IX.
com. = commissure between palatinus and maxillaris.
f. = frontalis.
fac. = facialis.
gph. = glossopharyngeal.
gas. gang. = ganglion of V and VII.
hy.man. = hyomandibularis.
man. = mandibularis.
men. = mentalis.
mas. = masseter.
n. = nasalis.
o c.m. = oculomotor.
ol. = olfactory.
op. = optic.
r.a.a. = ramulus acusticus anterior.
r.a.l. = " " exterior.
r.a.p. = " " posterior.
r a.bas. = " " basilaris.

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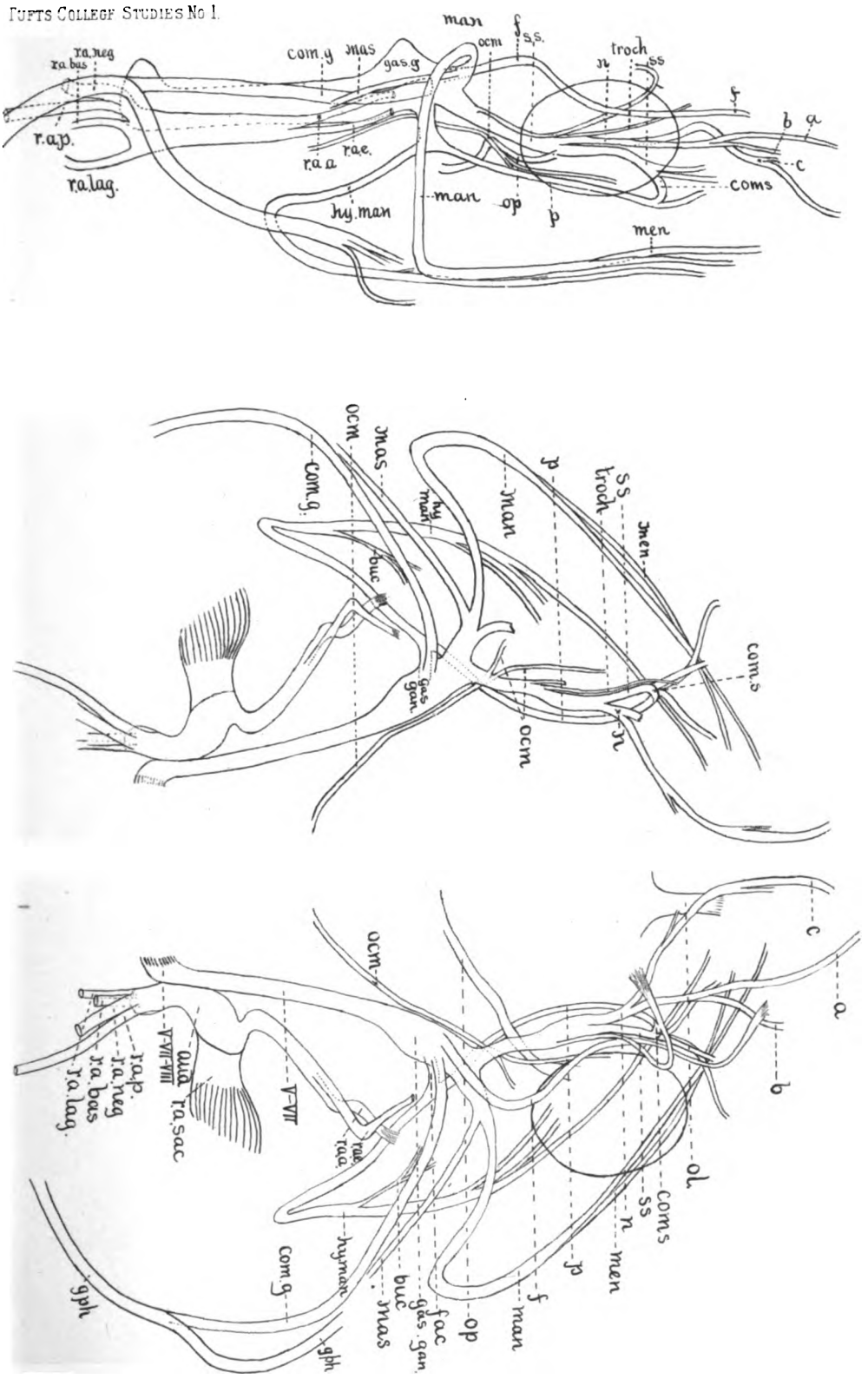

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r.a neg. = ramulus acusticus neglectus.
r.a.sac. = " " sacculi.
s.s. = supramaxillaris superior.
troch. = trochlearis.
V, VII, VIII = origin of V, VII, and VIII from brain.

FIG. 1. Nervous system of Pipa from the right side.
FIG. 2. Same from above. On the left side some of the more dorsal nerves are removed.

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ECTODERMIC ORIGIN OF THE CARTILAGES OF THE HEAD.[1]

BY JULIA B. PLATT.

This notice is merely preliminary to a paper which I hope soon to publish with illustrations and detailed descriptions.

The embryonic cells and nuclei of Necturus are very large, and at an early stage heavily laden with yolk, which, as the head of the embryo, is folded off, rapidly disappears from the differentiated tissues. The yolk granules, however, disappear much sooner from the ectodermic than from the entodermic tissues. A further consequence of the immense amount of yolk carried by the entoderm is that its activity is retarded as compared with the ectoderm. These differences affect not only the two primitive germ layers, but also the cells derived from these layers and constituting the so-called "middle layer"—the mesoderm.

These three factors, namely: 1st. The size of the cells and their nuclei; 2d. The natural differentiation of the two primitive tissues and their derivatives occassioned by the difference in the quantities of yolk they contain; 3d. The retarded activity of the entoderm cells, contribute to render Necturus an especially favorable object for the determination of the ectodermic origin of the head cartilages.

Before the closure of the neural folds, the ectoderm becomes thickened in two broad bands parallel to the long axis of the embryo, and extending backward from the anterior limits of the medullary plate. Dorsally, each band reaches nearly to the summit of the neural fold. Each is thickest near the dorsal wall of the mesodermic somites, and fades away as the ectoderm passes off laterally over the yolk.

Later, the anterior, or cranial portion of the band breaks up into a series of vertical ridges, each of which gives rise to a

[1] Reprinted from the Anatomischer Anzeiger, viii Jahrgang, No. 14 and 15, pp. 506–509, June 3, 1893.

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sensory epithelium followed by a region of cell proliferation in three directions: medianly to meet pockets from the entoderm with which the ectoderm fuses to from the gill clefts, and laterally into each of the adjacent gill arches, where the cells thus proliferated form dense masses with peculiarly round nuclei, readily recognized as the embryonic tissue from which later the cartilages of the gill arches are formed, and through which the blood spaces soon cut their way. Below the region in which the fusion with the entoderm takes place, the lateral proliferation of mesoderm into the branchial arches continues. We may thus distinguish in the ectodermic ridges three regions following one another dorso-ventrally as follows: 1st. The region of the sense organs; 2d. That of fusion with the entoderm and proliferation of mesoderm; 3. That of proliferation of mesoderm alone.

In the neighborhood of the nasal epithelium and posterior to the optic vesicle, similar mesodermic proliferations from the ectoderm are found, giving rise also in these regions to dense masses of cells with round nuclei—the Anlage of cartilage. The proliferation into the mesoderm is especially active around the mouth, as, owing to the cranial flexure, several lines of proliferation appear to meet in the angle where the mouth breaks through, and the formation of the trabecular cartilages may readily be followed.

As yet my study has not extended to the formation of the cartilages of the trunk, but homogeneousness of structure furnishes at least a presumption in favor of similarity of origin, otherwise one might be forced to doubt a fundamental difference between ectoderm and entoderm.

While the study of Elasmobranch, Teleost and Chick leads me to believe that like observations may be made in these forms, I know that, owing to the early wandering of cells from the walls of the mesodermic somites and the close approximation of these cells to the ectoderm, the important part played by the ectoderm in the proliferation of mesoderm for the formation of cartilage came to be traced as easily as in Necturus Nevertheless, Kastschenko[2] has observed the contribution of

[2] N. Kastschenko. Zur Entwickelung des Selachierembryos. Anatomischer Anzeiger, Bd. III.

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ectoderm to mesenchyme in Elasmobranchs, and Goronowitsch[3] notices a similar proliferation of ectoderm in the bird in the region of the nose, mouth, and branchial clefts.

In this connection I would call attention to a proliferation of ectoderm cells into the mesoderm noticed by Oppel[4] in *Anguis fragilis* and by myself[5] in Batrachus, and confirmed by the observations of H. B. Pollard on many forms of Teleosts at the Naples Station. The proliferation to which I refer is immediately back of the eye. It was interpreted by me (*loc. cit.*) as indicative of a lost gill-cleft, which may be still true, though the proliferation doubtless has reference to the dense mass of cells which lie immediately below it, and which constitute what Stöhr[6] calls "den Boden, in welchem sich der Processus pterygopalatinus entwickelt."

I would add that (as has been observed in several other Vertebrates) a large part of the sheet of neural cells which lies above and at the side of the first and second primary cerebral vesicles, and which, in part, forms the Anlage of the trigeminus group, breaks up in Necturus into stellate mesoderm. What rôle these cells play in the formation of later tissues I do not know, nor do I know what becomes of the "lost" portions of the neural crest which lie between the spinal ganglia, but it has become evident that the whole question of the nature of "mesoderm" in Vertebrate needs revision founded on *fact* rather than *theory*, and I doubt our right to co-ordinate the mesoderm with the two primitive germ layers—ectoderm and entoderm. I also doubt our wisdom in grouping together under a common name tissues so widely different in origin and fate.

[3] N. Goronowitsch. Die axiale und die laterale Kopfmetamerie der Vogelembryonen.—Die Rolle der sog. "Ganglienleisten" in Aufbau der Nervenstämme. Anatomischer Anzeiger, Bd. VII.

[4] A. Oppel. Ueber Vorderkopfsomiten und die Kopfhöhle von Anguis fragilis. Archiv f. mikrosk. Anatomie, Bd. XXXVI.

[5] Julia B. Platt. Further Contribution to the Morphology of the Vertebrate Head. Anatomischer Anzeiger, Bd. VI.—The double nature of the mouth involution mentioned in this paper was independently observed by me. Priority of observation, however, belongs to Miss Cornelia M. Clapp.

[6] P. Stöhr. Zur Entwickelungsgeschichte des Kopfskeletes der Teleostier. Leipzig, 1882.

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THE CLASSIFICATION OF THE ARTHROPODA.*

BY J. S. KINGSLEY.

In the concluding section of my paper on the Embryology of Limulus ('93), I expressed my views upon the classification of the Arthropods. The following is to be regarded as an expansion of the remarks I then made, with the inclusion of some matter not then available.

Since the days of von Siebold ('46), the naturalness of the group of Arthropoda has been almost universally recognized, only a few, like the present writer ('83) and von Kennel in his recent text-book of Zoology ('93), appearing to doubt the homogeneity of the division. On the other hand, the way in which the Arthropoda should be subdivided has been very differently regarded by different authors. Space will not permit an extended résumé of the growth of our knowledge, but it is fair to say that almost every person treating of the subject has added materially to the basis for a natural classification, either by the discovery of new facts or by throwing new light upon facts known before. At present, the great majority of naturalists divide the Arthropod phylum into two groups or sub-phyla, which, however named, are essentially Branchiata and Tracheata, the former embracing the Trilobites, Eurypterids, Hemiaspids and Xiphosures, along with the true Crustacea; the latter containing the Onychophora (Peripatus) Myriapods, Hexapods and Arachnids.

Yet this division is not universally accepted, and a few years ago, Professor E. Ray Lankester, following out the earlier suggestion of Strauss-Dürckheim and the later one of the younger van Beneden ('71), demonstrated that the affinities of Limulus were with the the Arachnids rather than with the Crustacea. This epoch-making paper—"Limulus an Arachnid"—must form the basis of all farther studies of Arthropod taxonomy, since it logically follows from his conclusions that the distinctions made between Branchiata and Tracheata are physiologi-

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cal rather than morphological, and that their emphasis tends to obscure true relationships upon which alone a natural system can be based. Since Lankester wrote, most students of Arachnid morphology and every one (excepting Professor Packard) who has investigated the structure or ontogeny of Limulus, have endorsed the general conclusion that Limulus is closely related to the Arachnids.

This being the case, Lankesters's later views upon the subdivision of the Arthropoda possess a peculiar interest. In the ninth edition of the Encyclopedia Britannica, article "Zoology," he gives the following arrangement:

Branch Arthropoda.
- Grade 1, Ceratophora.
  - Class I, Peripatidea.
  - Class II, Myriapoda.
  - Class III, Hexapoda.
- Grade 2, Acerata.
  - Class I, Crustacea.
  - Class II, Arachnida.
  - Class III, Pantopoda,
  - Class IV, Tardigrada.
  - Class V, Linguatulina.

Professor Claus is apparently not so radical in his ideas. I fail to make out from his various polemical articles ('86 [a, b]., 87 [a]) exactly what his later views are, but in the fourth edition of his Lehrbuch ('88)—the fifth edition is not at hand—there is such a lack of regularity in the subordination of type, headings, etc., that it is difficult to ascertain his opinions. As I interpret him, he has the following scheme:

Arthropoda.
- Class 1, Crustacea.
  - Sub-Class I, Entomostraca.
  - Sub-Class II, Malacostraca.
  - Gigantostraca.
    - Merostomata.
    - Xiphosura.
- Class II, Arachnoida.
- Class III, Onychophora.

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Class IV, Myriapoda.
Class V, Hexapoda.

From this it would seem that the only conclusions which can be drawn are that, at least at this date, Professor Claus regarded the Gigantostraca as a subdivision of the Crustacea, but was uncertain whether to regard it as equivalent to the Entomostraca and Malacostraca or not.

It is impossible to give the views of Hatschek, as the part of his "Zoologie" treating of the Arthropods has not yet appeared. In his general table ('88, p. 40) he accepts, in a modified way, the Articulata of Cuvier, and regards the Onychophora as a class, of equal rank with the Arthropoda.

The earlier studies of Boas upon the classification of the Crustacea possess such value that his general ideas upon the subdivisions of the Arthropoda deserve mention. In his "Zoologie" ('90) he adopts the following arrangement:

Arthropoda.
- I Class, Crustacea.
  - I Sub-Class Entomostraca, including as Orders: I, Phyllopoda; II, Cladocera; III, Xiphura (*sic*); IV, Trilobitæ; V, Ostracoda; VI, Copepoda; VII, Cirripedia.
  - II Sub-Class, Malacostraca.
- II Class, Myriapoda.
  - (Peripatus doubtful.)
- III Class, Insecta.
- IV Class, Arachnida.

Lang ('88) has the following classification:

Arthropoda.
- I Sub-Phylum, Branchiata.
  - Only class Crustacea.
    - First "Anhang" to Branchiata—Trilobita, Gigantostraca, Hemiaspidæ, and Xiphosura.
    - Second "Anhang"—Pantopoda.
- II Sub-Phylum, Tracheata.
  - I Class, Protracheata.
  - II Class, Antennata (Myriapoda and Hexapoda).
  - III Class, Chelicerotæ *sive* Arachnoidea.
    - "Anhang" to Arthropoda—Tardigrada.

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Fernald has approached the subject from the standpoint of Hexapod morphology. He gives ('90) a phylogenetic tree in which two main trunks arise from the primitive unsegmented worm. One of these embraces the Annelids and Peripatus, the other includes the Arthropods proper. This latter branches into the Hexapods and the Crustacea, the Arachnids and Limulus being represented as offshoots from the main Crustacean line. The origin of the Myriapods is left in doubt, but of the two divisions the Chilopods are represented as an offshoot from the Diplopod stem.

Richard Hertwig ('92) adopts the following scheme:

Branch Arthropoda.

I Sub-Phylum, I Class, Crustacea.

1 Sub-Class, Entomostraca, containg as regular members the Orders: I, Copepoda; II, Branchiopoda; III, Ostracoda; IV, Cirripedia; and, as "Anhangen," V, Xiphosura; VI, Trilobitæ; VII, Gigantostraca.

II Sub-Class, Malacostraca.

II Class, Onychophora.

III Class, Myriapoda.

IV Class, Arachnoida (including Pantopoda as an "Anhang").

V Class, Hexapoda.

Lastly, von Kennel, whose studies on Peripatus entitle his views on Arthropod taxonomy to a hearing, denies ('93) the validity of the group Arthropoda, claiming that those features which would seem to unite the Tracheata and Branchiata are either superficial or are common to the whole series of metameric Invertebrata. He places the Xiphosura among the Crustacea, apparently regarding them as equivalent to the rest of the group. The Tracheata are divided into three sub-classes, Myriapoda, Hexapoda and Arachnoida, the relationships of Tardigrada and the Pycnogonida being regarded as uncertain.

My own views, as stated in my last paper on Limulus, have not undergone any extensive modification, although the tabular statement has undergone some slight changes. Chief of these is the transfer of the Trilobitæ from a position of uncertainity to a more close union with the true Crustacea, a matter

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which will be referred to again below. I would now present the following scheme:

- Phylum Arthropoda.
  - Sub-Phylum I, Branchiata.
    - Class I, Crustacea.
      - Sub-Class I, Trilobitæ.
      - Sub-Class, II, Eucrustacea.
    - Class II, Acerata.
      - Sub-Class I, Gigantostraca.
      - Sub-Class II, Arachnida.
  - Sub-Phylum II, Insecta.
    - Class I, Chilopoda.
    - Class II, Hexapoda.
  - Sub-Phylum III, Diplopoda.
- Incertæ Sedes—
  - Pycnogonida.
  - Linguatulina.
  - Pauropoda.
  - Tardigrada.
  - Malacopoda.

The various papers by Lankester, McLeod, Laurie and myself have, I think, clearly shown that the older grouping of the Arthropoda into Branchiates and Tracheates is not justified by the facts of structure and ontogeny; that tracheæ are not homologous structures in all Arthropods which possess them, and that the old group of Tracheata is polyphyletic in origin. Since classification must represent the various lines of descent, the old must therefore go. There remain many points which must be investigated anew, but I feel confident that further research will support, in its main features, the classification adopted above, and considered more *in extenso* below.

PHYLUM ARTHROPODA.

I am not prepared to discuss the validity of this group, although for reasons that will appear below, I am inclined to believe the great divisions which I recognize are but remotely related to one another, and it may yet be proved, as I suggested several years ago ('83), and as von Kennel believes, that

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they have no common ancestor nearer than the Annelids. The jointed nature of the appendages offers no insuperable objection to this view, while the early phases of the egg, the formation of the germ layers, the structure of the alimentary canal, the morphology of the reproductive and excretory organs, as well as certain facts concerning the circulatory, respiratory and nervous systems are easiest explained upon such an hypothesis. The presence of compound eyes in branchiate and tracheate forms would, at first thought, be a strong argument for the older views, but these organs differ so greatly in their structure that it is easier to regard them as homoplastic organs (comparable in a way to the eyes of Cephalopods and Vertebrates) rather than as derivatives from a common compound ancestral visual organ. For our present purposes, the group of Arthropoda may be retained as a convenient assemblage, characterized in the following manner: Heteronomously segmented animals, with, typically, a pair of appendages to each somite; the whole enclosed in a chitinous segmented exoskeleton, the jointing of which extends to the appendages, thus justifying the term Arthropoda. The appendages, primitively locomotor in function, may be modified, on one or more somites, for the taking or commuting of food, for respiration, copulation, oviposition, sensation, fixation, etc. No circular layer of muscles in body wall; nervous system consisting of a pair of primitively supraœsophageal ganglia and a ventral chain of paired ganglia, of which one or more pairs may, in the course of development, be transferred to the prestomial region. Eyes, simple, aggregate, or compound, with, in some cases, an inversion of the retinal layer. Cœlom small, inconspicuous; circulatory organs consisting of a dorsal heart enclosed in a vascular pericardial sac; blood-vessels more or less evidently metameric, terminating in "lacunar" spaces. Respiration, either by the entire surface of the body or by specialized outgrowths or involutions of the same. Excretion, either by true nephridia or by Malpighian tubules, developed from either the mid- or the hind-gut. Reproductive organs consisting of gonads developed from the cœlomic walls and with modified nephridia serving as efferent ducts.

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In order that we may compare, part with part, the different forms of Arthropods, it becomes necessary to assume some basis of comparison, and apparently the only one available is that of the exact homology of the similarly situated metameres in the different groups, but here we meet with a difficulty. How can we be certain, for example, that somite 10 of the lobster is the exact homologue of somite 10 in the beetle? How can we tell that no somite has been lost in the evolution of these different lines? Perfect certainty is impossible, and we now know that in the serial comparisons of not more than five years ago, errors crept in, because there is a tendency of somites to become aborted or obsolete. This tendency is well-known in cases of Apus and Oniscus, where one of the anterior pairs of appendages is greatly reduced; and in Limulus, Scorpions, Moina, etc., where an anterior somite is not differentiated until after those behind it. In many forms there is an obliteration or a fusion of cœlomic cavities in the anterior region, the mesoderm flowing together as a common mass.

On the other hand, the embryonic phases of the nervous system seem to give clear indications of neuromeres in the anterior end of the body, and, as farther back, neuromeres correspond to the mesodermic metameres, it is reasonable to accept until error be shown, a somite for each neuromere at the anterior end of the Arthropod body. Unfortunately, we have detailed knowledge of these neuromeres in but few cases, and even in these there is a lack of uniformity in the observations.

In the Hexapods it has been shown that the "cerebrum" of the adult is composed of at least three pairs of ganglia called by Vaillanes, respectively, the protocerebrum, the deutocerebrum and the tritocerebrum. These elements have been recognized by Tichomiroff in the silkworm (teste Cholodkowsky) in Acilius (Patten, '88), in Blatta (Cholodkowsky, '91), in Mantis (Vaillanes, '91), in Xiphidium and Anurida (Wheeler, '93), while Carrière ('90) has described *four* cerebral elements in Chalicoderma. The figures of the latter author do not seem to me conclusive, and I am inclined to believe the more numerous observations in this difficult field as the more probably correct.

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These cerebral elements apparently have different values. So far as observations go, the protocerebrum is always preoral, and in no case is any appendage developed in connection with it. Apparently, the region in which it occurs is to be compared to the preoral lobe of the annelids, while the two ganglia of which it is composed would correspond to the "Scheitelplatte" of German embryologists. The other cerebral elements, on the other hand, are primitively behind the stomodæum, and, in some forms at least, an appendage is developed in connection with each. Thus the antennæ belong to the deutocerebral neuromere, while in Anurida Wheeler has shown that the tritocerebral neuromere possesses at an early stage a pair of small appendages, which here, as in all Hexapods, is absent from the adult.

In the Crustacea, not a few observations go to show somewhat similar conditions. We find there a protocerebrum without appendages at any stage, followed by a series of ganglia which present many claims to belong to the postoral series. In a paper on the Embryology of Crangon ('89), I claimed that in that form the antennæ were primitively postoral, but since the validity of my observations have recently been questioned by Weldon ('92) and Herrick ('92),[1] they must be repeated before they can be accepted. Aside, however, from these questionable observations, there are many other facts which go to show that the antennal neuromeres belong to the the postoral rather than to the prestomial series. There is, however, less evidence for this position for that pair of ganglia which exist in the lobster (see Bumpus ('91), pl. XVII, fig. 1), between the protocerebral ganglia and the neuromeres of the antennæ. It is without appendages, and although its fate has not been traced, it probably becomes fused in the "cerebrum" of the adult.[2] This neuromere is, I am inclined to think, also to be regarded as belonging to the same series as that of the antennæ.

[1] For some remarks upon these criticisms, see my paper ('93), p. 235, foot-note.

[2] Professor J. P. McMurrich informs me that he has found these deutocerebral ganglia in the various Isopods (Jæra, Oniscus, Porcellio, Armadillidium, etc.) which he has studied.

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In the Arachnids and the Xiphosures, we have evidence of several elements in the "brain." Both Patten and myself have shown the existence of three pairs of cerebral ganglia in Limulus, in front of the ganglia of the first pair of appendages. Patten finds ('90) the same number in the brain of the Scorpion, as do Locy ('86, pl. XI, fig. 70) and Kishenouyi ('90) in Agalena. The copies of Morin's figures given by Korschelt and Heider ('92, fig. 383 B) seem also to be in full harmony. On the other hand, Schimkewitsch (87, pl. XXI, fig. 3) represents two pairs of ganglia in Epeira in front of the ganglia of the first pair of appendages, while in the diagrammatic figure (pl. XXIII, fig. 5) he apparently indicates four pairs of preappendicular ganglia.

In other groups of Arthropods I know of no detailed observations which can be used to aid in the enumeration of the neuromeres in the anterior region of the body. If we assume that in the cases of Hexapods, Crustacea, Xiphosures and Arachnids, the neuromeres enumerated above represent the total somites in this region, we may then compare, somite by by somite, these groups in the following manner:

	HEXAPOD.	ARACHNID.	XIPHOSURE.	CRUSTACEA.
Neuromere I	No Appendage	No Appendage	No Appendage	No Appendage
" II	Antenna	No Appendage	No Appendage	No Appendage
" III	Appendage	No Appendage	No Appendage	Antennula
" IV	Mandible	Chelicera	1st Leg	Antenna
" V	Maxilla	Pedipalpus	2d Leg	Mandible
" VI	Labium	1st Leg	3d Leg	Maxilla 1
" VII	1st Leg	2d Leg	4th Leg	Maxilla 2
" VIII	2d Leg	3d Leg	5th Leg	Maxilliped 1
" IX	3d Leg	4th Leg	6th Leg	Maxilliped 2

Of course it will be understood that this grouping is limited by our present knowledge, and that at any time discoveries may be made which will overturn it. It is, however, to be noted that it brings the hinder margins of the thorax of the Hexapoda and of the cephalothorax of Limulus and of the

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Arachnids into exact correspondence. In the case of the Crustacea the corresponding line passes behind the third maxilliped of the Decapod.

If it should, however, be shown (as many believe) that the Crustacean metastoma has its own somite, the line will be thrown forward to behind the second maxilliped, and it will correspond to the line of division between the head and thorax of the Edriophthalmia.

Since the older ideas of numerical sequence are better known, I have used them in the following discussion rather than that based upon the neuromeres. Thus in the Hexapods somite (or appendage) I=Neuromere II; in the Arachnid and Xiphosures somite I = Neuromere IV; in the Crustacea somite I = Neuromere III.

The morphology of some other organs call for a moments' consideration. Prominent among these are the vasa Malpighii. These are usually regarded as characteristic of the "Tracheates," and their presence in the Arachnids has been adduced as a strong argument for their association with the Hexapods. It has been, however, pretty conclusively shown that these organs are not homologous throughout the Arthropod phylum, for in the Hexapod they are derived from the hind-gut, and are therefore ectodermal, while in the Arachnida, as Loman ('86–7) has shown, they are derivatives of the mesenteron and are consequently entodermal. Their similarities are those of homoplassy rather than of homology, and the only argument that can be drawn from the occurrence in these forms is that Arachnids and Hexapods are not closely related. Similar organs with similar functions have been described in various Edriophthalmia, but we are yet in doubt as to their origin. The studies of Spencer ('85) represent them as without chitinous intima in the Amphipods. They may, therefore, be entodermal. A detailed study of the region of the hind-gut of certain Decapods might give results interesting in this connection.

The tracheæ furnished another instance of homoplassy. These organs furnish the chief ground for the group called "Tracheates," since in most they form the sole means of res-

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piration. Yet these are, in the opinion of many, not homologous. In the Hexapoda they arise, ontogenetically, as inpushings of the ectoderm of sides of the body, outside and above the line of the insertion of the limbs. Their method of growth, the general structure, etc., all point to their origin, as was pointed out by Chun ('75) from dermal glands which later assumed respiratory functions. The tracheæ of the Arachnids, on the other hand, have had a different origin. In those forms in which they have been studied, they arise as inpushings behind the temporary appendages on the abdomen. There is not a little evidence to show that they have arisen from gills borne on the posterior surfaces of these appendages, as in the Limulus of to-day; that they have been pushed into the body, taking the form of lung books, a condition permanent in all the respiratory organs of the Scorpions and in those of one or two somites of the Araneina; and then, coincidently with a reduction in the circulatory organs, they have penetrated farther and farther into the body. For the details of this process, as well as for the wonderful histological similarity between the embryonic gills of Limulus and lungs of Arachnids the reader is referred to my full paper. The "spiral threads" in the two cases are to be explained as mechanical in origin—corrugations give greater strength without excessively thickening the intima. Still, a third type of "trachea" is to be be found in the gills of the Oniscid Crustacea. These organs have become adapted for aerial respiration, and, in connection with this change, the organs have been permeated by branches of minute tubes, lined with a chitinous intima, produced by inpushings of the outer body wall. These tracheæ cannot be regarded by the strongest advocate of the naturalness of the "Tracheates" as homologous (*i. e.*, homogenous) with those of the Hexapods. I have made a number of, as yet unpublished observations on these organs in Porcellio. Leydig described, them in detail some years ago ('78). The peculiar structures in the genus Tylos as described by Henri Milne-Edwards ('40, p. 187–8) should be considered in this connection.

It is only recently that the existence of nephridia in the Arthropoda has been placed beyond a doubt. The earlier students

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of the shell gland of the Entomostraca often made comparisons between it and the "segmental organs" of the Annelids, but the trouble was that the former terminated blindly internally, while in the Annelids the organ formed a tube connecting the body cavity (cœlom) with the interior. The problem was solved by Sedgwick ('88), who showed that in Peripatus the nephridia were closed internally, but that they were still nephridia as proved by development, and that we have here to deal with a greatly diminished cœlom. In the light of these facts it is now placed beyond a doubt that in the antennal and shell glands of the Crustacea, and in the coxal glands of Arachnids and Limulus, we have true nephridia.[3] In all there is the formation of a cœlom, a division of the cœlom of certain somites into dorsal and ventral moieties, and a development of the lower portion into end sac and nephridial tube, the latter portion breaking through to the exterior.[3]

Following the discoveries by Sedgwick that the genital ducts of Peripatus were modified nephridia, came the observations of Heymons ('90), Cholodkowsky ('91) and Wheeler ('93), all of which show that exactly the same conditions exist in the Hexapods, while Laurie ('90) has demonstrated that it is at least probable that the same holds true for the Scorpions. I made no observations on the origin of the genital ducts of Limulus, and I do not recall any account of their development in the Crustacea. In the latter group, however, there is not a little evidence of an anatomical character which is easiest interpreted upon the same hypothesis. There these ducts are metameric, and may occur in different somites in the different sexes. This condition is to be explained in two ways, as has previously been pointed out by Lankester. Either the ducts are to be regarded as new formations, or they are previously existing structures modified for reproductive functions exclusively. That this latter is the case, and that the ducts are nephridial is rendered probable by the following considera-

[3] These organs have been shown beyond a doubt to be mesodermal by Grobben ('79), Kingsley ('89, '90 and '93), Kishenouyi ('91), Lebedinsky ('92), Laurie ('90), etc., and yet Bernard ('93), with these facts available, has recently attempted to derive these structures from the glands of annelids—ectodermal structures—ignoring the facts presented by those who have actually investigated the subject.

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tions: In all metameric animals one or more pairs of nephridia serve as genital ducts, and no case is known of the formation of new outlets. The genital ducts are so related to the gonads and these latter to the cœlom, at least in the Decapods (*cf.* Weldon, '89, '91) that we must regard the genital epithelium as cœlomic, and the ducts as ventral diverticula of the same space.

The salivary glands afford some difficulties, for they occur in most "Tracheates," and are usually stated to be absent from the "Branchiates." This apparent difference between the two groups is possibly to be explained by the different method of life—aquatic in the latter, terrestrial in the former. It is, however, to be noted that salivary glands have been recognized in Astacus (*cf.* Lang, '89, p. 344), while renewed studies must be made of the so-called salivary glands of the Arachnida before we are certain of their homology with those of the Hexapods. Several organs which have been called salivary glands among the spiders and their allies have been shown to be coxal glands (*i. e.* nephridia) or poison glands, and it is possible that all of these organs may have different homologies than those indicated by the name usually applied to them.

A group of structures which cannot, as yet, be discussed, is that of the embryonic membranes. In the Scorpions as in the Hexapods, the embryo develops those as yet unexplained fœtal membranes which so closely simulate those of the higher vertebrates. It may be that here, as in other places, we have similar but not identical organs. The accounts of their development in the Arachnids by Metschnikoff, Kowalevsky and Schulgin, and Laurie differ considerably, and, until we know something of the ancestry and real meaning of the structures which are united under this head we cannot be certain of the taxonomic value to be placed upon them. It may be noted here that the structures described by Bruce ('87) as occurring in the spiders are, in all probability, not amnion and serosa, but either invaginations in connection with the brain or the inpushing to form the median eye.

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SUB-PHYLUM I—BRANCHIATA.

Arthropods breathing by means of gills (or lungs or tracheæ modified from gills) developed in connection with the appendages; without distinctly differentiated head, with long stomodæum, nephridia persisting in somite II or V (or both), genital ducts opening near the middle of the body. Anterior appendages all multiarticulate, the basal joints of one or more pairs serving as organs of manducation. A chitinous entosternite and deutova frequently present.

I hardly think it necessary, each time the limits of a group are changed, to give the new combination a new name. Our nomenclature is already cumbersome enough, and the slight indefiniteness is vastly preferable to the confusion of the other course. I have, therefore, retained the term Branchiata for the enlarged group, since I regard the lungs and tracheæ of the Arachnids as but modified branchiæ. In only the Edriophthalmia and certain Phyllopods do we have a distinctly differentiated "head," and the head in these groups is not the same in its limits. Under the head of nephridia I include the antennal and shell glands of the Crustacea and the coxal glands of the Arachnids and Limulus. The former have been shown by numerous observers to be true nephridia, while the observations of Laurie ('90) and Lebedinsky ('92), Sturanay ('91), are conclusive to the Arachnids. The observations of Gulland ('85), Kishenouyi ('91) and myself ('85 and '93) would seem to settle the matter in the Horse-shoe crab.[4] That the genital ducts are to be regarded as modified Nephridia has already been shown. Their position is inconstant in the Crustacea, varying in some forms with the sexes of the same species. In some of the more reduced forms, as the cirripeds, they are apparently almost terminal, a condition to be explained by the

[4] In my first paper on the development of Limulus, I pointed out that the coxal glands of Scorpio and Limulus were apparently homologous with the shell gland of the lower Crustacea, since in both cases they open at the base of the fifth pair of appendages. This identification is apparently not pleasing to Professor Claus ('86,) since he has seen fit to ridicule my ideas of homology. I confess that I do not understand his objections, and certainly the evidence derived from the neuromeres (admitting one for metastoma of the Crustacea—*cf.* Brooks, '82), seems fully to support my thesis.

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small number of metameres that become differentiated. Other features which are common to most Branchiates, but which either are not common to all or are at the same time common to some of other groups, will appear below. It must, of course, be understood that in the above diagnosis of the group, features of internal anatomy are known only of recent forms; of the visceral structure of the trilobites, we are absolutely in the dark.

CLASS I—CRUSTACEA.

Branchiate Arthropoda with functional gills; with one or two pairs of distinctly preoral appendages (antennæ) the first being purely sensory; the ganglia corresponding to these appendages being fused with the protocerebrum to form the "brain;" the appendages with typically a basal joint giving rise to two or three branches; several pairs of appendages modified for eating; alimentary canal with long œsophagus and well-developed stomodeal "stomach," mid-gut region short, the mid-gut glands ("liver") being well-developed; proctodeum long.

In all living Crustacea (Eucrustacea), there are two pairs of antennæ, although in some forms (e. g., Apus, Oniscids) one or the other pair has has become greatly reduced. In the Trilobites, on the other hand, but a single pair has, as yet, been discovered. It therefore remains to be shown whether a single pair is characteristic of these forms, or whether we have here a possibly greatly reduced additional pair. In case the former alternative prove true, it may be necessary to remove the Trilobites completely from the position here assigned them, though it will not necessarily follow that they should be associated with the Eurypterids and Limulus. (For the position of the Trilobites, see below).

It is difficult to say exactly what weight should be given the so-called "typical Crustacean limb," the di- or trichotomous appendage so frequently met with in this class, and which is not infrequently regarded as diagnostic. That this condition is a derivation of the lamellate condition found in Apus, as maintained by Lankester ('81) admits of little doubt, and

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hardly more doubtful is the view which would compare the Phyllopod appendage with the Annelid parapodium. But two- and three-branched appendages are not unknown outside the Crustacea. One of the arguments advanced in favor of a Crustacean position for Limulus is that the abdominal appendages in that form are two-branched, but numerous observers have recorded a biramous condition in the appendages of the young of various "Tracheates." Among others we would mention the biramous pedipalps in Dendryphantes recorded by Croneberg ('80), the biflagellate antenna of an Indian Lepisma, and of an embryo *Blatta javanica* by Wood-Mason ('79), the bifid condition of the antenna of Blatta by Wheeler ('89), while Patten ('84), in the same form, describes the maxillæ and labium as "formed respectively of two and three branches, the second maxillæ thus attaining the typical trichotomous structure of the Crustacean appendages." Similar observations have been made upon other Hexapods, while in the Pauropida the trichotomous antennæ are to be called to mind.

Fully as characteristic is the extreme reduction of the entodermal portion of the alimentary canal proper, the entoderm cells being largely confined to the liver or mid-gut gland, while the canal itself is almost entirely composed of stomodeal and proctodeal invaginations (*cf* Kingsley, '89, pp. 13-19).

SUB-CLASS I—TRILOBITÆ OR PALÆOCARIDA.[5]

Fossil Crustacea with tri-regional body—head, thorax, pygidium, all bearing appendages. "Head" unsegmented, with one pair of antennæ and with four pairs of postoral appendages, all pediform and with basal points manducatory. Thoracic somites indefinite in number, each bearing a pair of biramous (exopodite and endopodite) appendages, each appendage provided with a straight or curiously coiled gill (?). Pygidium segmented, with appendages beneath.

For several years I have maintained that the Trilobites had but the most distant affinities with the Xiphosures (e. g., '85, p. 555).

[5] This term was introduced by Packard ('79) for Limulus, the Trilobites and the Eurypterids. Later ('86), with no apparent reason, he dropped this term and substituted for it Podostomata. The two groups, as he limits them, are exactly the same.

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In my latest paper ('93, pp. 252–254) I repeated the same ideas, and, within a short time of this paper, appeared Mr. Matthew's notice ('93) of the existence of true Crustacean antennæ in these forms. This, combined with the truly Crustacean thoracic appendages already described by Wolcott ('81 and' 84), and the utter inability, upon careful analysis, to homologise the regions in Limulus and the Trilobites, is sufficient to divorce the two and to assign the latter to the Crustacea.

Exactly what position they should occupy here is uncertain. It is undeniable that they present a superficial resemblance to the Isopoda. In both there is the same depressed body, the division of this into the three regions of head, thorax and abdomen, the head in both cases bearing sessile compound eyes; but at this point the resemblance ceases. In the Isopod the thorax is always 7-jointed; in the the Trilobites the number varies very considerably. In the Trilobites the appendages, as restored by Walcott, surround the mouth, much as in Limulus or the Scorpions; in the Isopods the arrangement is truly Crustacean. In the Isopods, in the embryo, as well as in the adult, the thoracic appendages consist of but a single branch, and when any other structures are present, as for instance, the plates forming the brood-pouch, these are placed mediad to the insertion of the limb; the gills (?) in the Trilobites are outside the point of articulation, while the limbs, as already stated, are dichotomously branched. In the Isopods the respiratory organs are lamellar appendicular plates beneath the abdomen; we do not know exactly what structures are found here in the Trilobites. Professor Mickleborough ('83) thinks that there are lamellar plates, but Mr. Walcott ('84) studying the same specimens believes that the appendages of this region resemble those of the thorax.[6] So it would appear that the Trilobites have no close affinities with the Isopoda; the resemblances to the Amphipods are even less close. So far as I am aware, there is no recent Crustacean which presents any resemblance to Trilobites closer than those of the Edrophthalmia just discussed, and yet we

[6] The process cuts illustrating Mr. Matthew's article gives no intelligible details of the foot structure in Triarthrus.

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must consider these forms considerably removed from the primitive Crustacean stock, which, in the opinion of many, was not far removed from the modern Phyllopoda. Both types are well differentiated in the lower Cambrian, and no fossils as yet discovered serve to bridge the gap between the two. Nor does the little known of Trilobitan embryology throw any light upon the question. In some there is an apparent close similarity to the early stages of Limulus, but this may easily be explained upon the general principles of Arthropod growth. Thus, in Sao, as described by Barrande ('52), in which the resemblance to the Xiphosures is most marked, we have but that increase in the number of somites from a posterior budding zone common to most Arthropods, while in Trinucleus (Barrande) there seems to have been an acceleration in the development of cephalic and pygidial regions, and then, later, an increase in the number of thoracic segments in that manner so familiar in the development of the Decapoda. The resemblances to Limulus all lie in the depressed body form and the union of the anterior somites.

SUB-CLASS II—EUCRUSTACEA.

Crustacea, with filiform, plumose or lamellate gills, in either thoracic or abdominal region; mouth parts never ambulatory in the adult, but modified for the prehension and comminution of food. Nauplius stage either free-swimming or passed in the egg.

It is difficult, with our present knowledge, to find good diagnostic points separating the true Crustacea from the Trilobites, and it may be that further research will show that the latter are to be regarded as a division equivalent to some of those mentioned below. At present, the arrangment of the feet of the cephalic region in a circle around the mouth, the use of their basal joints for the comminution food, and the apparent functioning of the distal joints as locomotor organs, together with the peculiar gills, must serve to differentiate the two groups, it being understood that the ideas here expressed are merely provisional.

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In the sub-division of the Crustacea I am inclined to adopt the recent "sub-classes" of Grobben ('92) as super-orders as follows:

Super-Order I, Phyllopoda.
  Order I, Euphyllopoda.
  Order II, Cladocera.
Super-Order II, Estheriæformes.
  Order I, Ostracoda.
Super-Order III, Apodiformes.
  Order I, Copepoda.
  Order II, Cirripedia.
Super-Order IV, Malacostraca sive Branchipodiformes.
  Order I, Nebaliadæ. I, Leptostraca. II, Eumalacostraca.
  Order I, Stomatopoda.
  Order II, Thoracostraca.
  Order III, Arthrostraca.

On the whole, I accept the conclusions of Grobben as to the relationships of the various groups, and have, like many other zoologists, regarded the Phyllopods as the ancestral stock. I think that this is shown by, among other points, the structure of the appendages, regarding which I fully accept the conclusions of Lankester[8] ('81). I do not regard the nauplius stage as indicative of a naupliform ancestor, but as an introduced feature, for which view the arguments adduced by Claus and Dohrn, seem valid. The ancestor of the Phyllopods must have been an elongate poly-somitic animal with lamellate appendages, the basal portions of one or more "legs" serving at the same time as both locomotor and manducatory organs. In

[7] I regard Packard's ('87) Syncarida as a group of Amphipoda of scarcely more than family rank.

[8] Grobben does not accept Lankester's views, and claims that embryology shows that Lankester's sixth endite is the endopodite and the flabellum the exopodite, in support of which he cites the observations of Claus ('73, p. 20). I cannot find there or anywhere else in Claus' paper any evidence which is not capable of being interpreted in full harmony with Lankester's view that the 5th and 6th endites of the Phyllopod limb are endopodite and exopodite respectively, while the flabellum is the homologue of the epipodite of the "typical" Crustacean limb.

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short, my views as to the ancestral form are much like those adopted by Bernard ('92), although I cannot accept all of his conclusions as to the steps of the evolution.

CLASS II—ACERATA.

Branchiate Arthropods, in which the branchial folds, developed from the abdominal appendages function as gills, as lungs, or as tracheæ. The body is divided into cephalothorax and abdomen, the line passing behind the sixth pair of appendages. The genital ducts open upon the first abdominal somite. The anterior postoral ganglia unite to form a ganglionic ring aronnd the œsophagus; the median eyes are invaginate. The entoderm (at least in several types) arises by delamination; there is a large mid-gut, with well-developed glands ("liver") while the proctodeum is short. The genital glands are reticulate and the spermatozoa are motile.

There is little to be said upon the foregoing points, to which many more, applicable to both Xiphosures and some Arachnids, might be added. The exact serial correspondence of the respiratory metameres in Limulus and the Scorpions have been enlarged upon by Lankester ('81[a]), and considerable emphasis must be placed npon the fact that in all Arachnids the stomata are ventral, and are, in all instances, except in possibly the Solpugids and a few mites, are confined to the abdomen. These exceptions need new study. In the Scorpion, as in Limulus, the observations of Narayanan ('89) and Laurie ('90) show that the genital ducts are modified nephridia, and that they open upon the posterior surface of the first abdominal appendages. Delamination has been shown to occur in the Pseudoscorpions, Araneina, Phalangids and Limulus, as well as in the doubtfully Arachnidan Pycnogonids.

SUB-CLASS I—GIGANTOSTRACA SEU MEROSTOMATA.

Six pairs of cephalothoracic limbs around the mouth, the bases of the posterior pairs being masticatory. Behind the mouth a metastomial plate or pair of plates. Anterior edge of carapax acute, its upper surface bearing median ocelli and

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a pair of lateral compound eyes. Respiration by means of lamellate branchiæ (gill books) borne on appendages 2–6 of the abdomen and protected by the enlarged first pair (operculum) which covers them.

To these points, which cover both Xiphosures and Eurypterids, the following, derived from Limulus, may be added: No salivary glands, no Malpighian tubes, no embryonic membranes (amnion).

In this sub-class two orders are to be recognized, the Eurypterida (fossil) and the Xiphosures. In the latter are included the recent and fossil Limuloid forms. The difference between these is not readily formulated, but is readily recognized in the specimens. The affinities of Cyclus are uncertain.

Order I—Xiphosura.

Cephalothorax large, metastoma paired, telson elongate and spiniform,

Sub Order I—Limulidæ.

Abdominal somites six, coalesced.

Sub-Order II—Hemiaspida.

Abdominal somites more than six, free.

Order II—Eurypterida.

Cephalothorax small, abdomen large and elongate, twelve-jointed, the joints free, telson spatulate, metastoma unpaired.

SUB-CLASS II—ARACHNIDA.

Respiration by internal lungs or tracheæ, no compound eyes; entodermal Malpighian tubes present; Embryonic membrane (amnion) present in some.

I regard the Scorpionida as the most primitive type of Arachnida existing to-day, and the Acarina as the farthest removed from the original stem. This position of the Scorpions is shown by many facts of structure; and the pulmonate type of respiration—intermediate between the gills of the Gigantostraca and the tracheæ of the higher Arachnids—occuring in these forms is just what we should expect if the line of descent is, as here maintained, from branchiate forms. On the other hypothesis of a common origin of all "Tracheates" from some Peripatoid form, we should have the strange spectacle of

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the most primitive of all Arachnids with the most differentiated respiratory system.

In the Arachnida I recognize the following orders:[9]—I, Scorpionida; II, Thelyphonida; III, Araneida, IV, Solpugida;[10] V, Pseudoscorpii; VI, Phalangida; VIII, Acarina.

It is interesting to note in this connection that Pocock, on morphological grounds points out (Ann. & Mag, Nat. Hist., VI, xi, p. 2) that "the immediate ancestor of the Arachnida was constructed somewhat as follows: The body was composed of eighteen somites, the anterior of which were provided with large appendages set apart for locomotion and the prehension and mastication of food; the terga of this cephalothoracic region were fused to form a single shield or carapace, supporting a submedian and a cluster of lateral eyes at each side, and the ventral surface of the carapace [? cephalothorax], at least in its posterior half, was protected by a sternal plate. Each of the succeeding six somites bore a pair of small ventral appendages, and the generative aperture opened upon the sternal area of the first of these somites. The posterior six somites had lost their appendages, were probably narrower than the rest, and constituted a limbless caudal portion of the body, the last of them being furnished with a single plate, articulated above the anal aperature." This should be compared with one of the Eurypterida.

SUB-PHYLUM II—INSECTA SIVE ANTENNATA.

Arthropods with differentiated head consisting of procephalic lobes and four (five[11]) somites; head with somites anchylosed and provided with four pairs of appendages modified for sensation or for feeding; respiration by means of tracheæ (mod-

[9] In this I follow the order of Pocock (Ann. & Mag. N. H., Jan., 1893). His "sub-classes" Ctenophora, Lipoctena and super ordinal divisions Chaulogastra, Mycetophora and Holostomata are hardly to be regarded as of phylogenetic value.

[10] No group of Arachnids will better repay study than this. I do not believe that the distinction between the "head" and the "thorax" with its three distinct somites indicates any affinities with the Hexapods, but that the conditions here existing are to be best explained upon the ground of homoplassy. The position of the anterior stigmata in the first thoracic somite is of great interest,

[11] See p. 21.

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ified glands) opening to the exterior on the sides of the body in the post-cephalic region. Nephridia absent, except as genital ducts, which open near the posterior extremity of the body. Ectodermal Malpighian tubes present. Spermatozoa motile.

So far as I am aware, the dissolution of the old group Myriapoda and the union of the Chilopoda with the Hexapoda was first proposed by Pocock ('87). At about the same time, I taught the same view to my classes, and later ('88) published the same. Subsequently both Pocock ('93) and I ('93, p. 248 ff.) repeated our views within a month of each other.[12] This step, it seems to me, is fully justified. The affinities of the Chilopods to the Hexapods are most close, while those of Chilopoda and Chilognatha are quite obscure. There has been no greater stumbling-block for morphologists than the attempt to homologise the somites of millipeds and centipedes. Attempts to bring other organs into harmony are equally futile. The three groups under discussion may be contrasted as follows, it being of course admitted that we know next to nothing of the somites and serial homologies of either Diplopod or Chilopod, and that possibly future research will modify some of the statements below.

The Diplopod head bears, besides the antennæ, but two pairs of appendages—a pair of mandibles and a lower lip, composed of a pair of coalesced maxillæ.[13] In the Chilopod the conditions are as in the Hexapod, two pairs of maxillæ being present.

In the Chilopods, as in the Hexapods, each somite bears a single pair of appendages, while in the Diplopods the majority of the segments bear two pairs of appendages, and the researches of Heathcote ('88) show that each segment is, in reality, composed of two coalesced somites, a condition without

[12] One of our best students of the Myriapoda, the late C. H. Bollman, accepted my views and they appear in the posthumous collection of his papers ('93).

[13] The attempt made to show that this lower lip is composed of the two coalesced lower jaws, or first and second maxillæ, of the Chilognaths receives no support from the embryology of Julus (Heathcote '88), where there is but a single somite when the hypothesis calls for two. Further the innervation of the sense organs of the lower lip (*cf.* vom Rath, '86, Pl. XX, Fig. 1) shows that but a single pair of appendages is concerned in the part.

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parallel elsewhere in the Arthropoda. In the Chilopods there is a wide sternum separating the coxæ of the ambulatory appendages; in the Diplopods the coxæ are approximate, and the sternum is exceeding narrow, or even entirely absent.

In the Chilopods the stigmata, a pair to a somite, are lateral (dorsal in Scutigera), and are placed above and outside the insertion of the limbs, exactly as in the Hexapods. The tracheæ which arise from them are branched, and the intima is thrown into a well-developed spiral thickening as in the six-footed insects. In the Diplopoda, on the other hand, the stigmata are beneath the body[14] close to the legs, while the tracheæ (except in the Glomeridæ) are tufted and unbranched, and the thickening of the intima is poorly developed.

In the Diplopods there are well-developed foramina repugnatoria upon the sides of each somite of the body. Such structures are absent from the Chilopods (as from the Hexapods), except in a few Geophilidæ, where repugnatorial glands occur, opening by foramina in the mid-ventral line.

In the Chilopods the reproductive organs consist of paired[15] gonads situated above the alimentary canal and opening to the exterior by ducts which are at first paired, but which later unite into a common tube which leads to a single external opening situated in the penultimate segment of the body. In the Hexapods the conditions are almost exactly the same; the gonads are dorsal, the genital ducts unite (except in Ephemeridæ), and there is a single external opening, always at the posterior end of the abdomen. In both Hexapods and Chilopods the spermatozoa are motile. In the Diplopods there is a single unpaired gonad, situated beneath the alimentary canal, and the genital duct, passing forward, divides into two, each of which has its own opening at the bases of the legs of the second post cephalic segment. The spermatozoa are quiescent.

We know so little of the embryology of the Myriapods that the aid of development can be had to only a slight extent in our comparisons, but the facts which it affords seem important.

[14] In former papers I have said that the spiracles might be even *in* the coxæ. I recall having seen this statement but recently rather rather extensive reading of Myriapod literature fails to reveal my authority.

[15] Single in Scolopendra.

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In the Chilopods the embryo escapes from the egg with numerous ambulatory appendages, a pair to each somite. The same is true of the typical Hexapods, all later observers agreeing that a polypod precedes a hexapod condition. The young Diplopod escapes from the egg in a Hexapod condition, and the presence of these six legs has been seized upon as a proof of the near association of these forms. An exact comparison, however, seems to show that the two are in reality very unlike as appears in the following table.[16]

	HEXAPODA (+CHILOPOD).		DIPLOPOD.	
Appendage I	Antenna	Head	Antenna	Head
" II	Mandible		Mandible	
" III	Maxilla 1		Lower Lip	
" IV	Maxilla 2		Foot 1	
" V	Thoracic Foot 1	Thorax	Absent	
" VI	Thoracic Foot 2		Foot 2	
" VII	Thoracic Foot 3		Foot 3	
" VIII	Abdominal Foot 1		Absent	
" IX	Abdominal Foot 2		Absent	

CLASS I—CHILOPODA.

Insecta with elongate depressed body, no differentiation between thorax and abdomen, all the somites being provided with appendages, those of the thorax-abdomen being locomotor in function.

CLASS II—HEXAPODA.

Insecta with body consisting of not over 19 somites, divided into head, three-jointed thorax and abdomen. Thorax provided with three pairs of locomotor appendages, and usually with two pairs of wings; abdominal appendages usually lacking from most somites, those of the extremity being usually

[16]As nothing is known of the existence of a tritocerebral segment in the Diplopods, the comparison can only be made upon the basis of the appendages of the adult. If the tritocerebral segment should prove lacking in the millepeds, the contrast will prove stronger than it now is. The statement of the Diplopod appendages is based upon Heathcote ('88).

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modified for reproduction and sensory purposes, those of the other somites, when present, being weak.

SUB-PHYLUM III—DIPLOPODA SIVE CHILOGNATHA.

Elongate, homonomously segmented Arthropods; head distinct, bearing three pairs of appendages; no distinction between thorax and abdomen; this region with numerous somites, all, except the anterior, having two pairs of appendages (double somites), sternum narrow. Stigmata two to each somite, tracheæ tufted and unbranched, not anastomosing. Gonads single, beneath the alimentary canal; spermatoza quiescent; genital ducts opening between the bases of the second and third pairs of feet.

I have given above my reasons for the separation of the Diplopods from the Chilopods, and need not repeat them here. I do not discuss the relations of the Diplopoda to the other sub-phyla, nor the relative position to be accorded the group. The ventral position of the gonads is a mark of low rank, but in other respects the organization is much higher.

ARTHROPODA OF UNCERTAIN POSITION.

I—PYCNOGONIDA SIVE PANTOPODA.

Regarding the systematic position of these forms I cannot add anything to the remarks of Morgan ('90), who has shown that not only in adult structure but in certain features of development, notably in the formation of the entoderm by delamination, they present conditions not easily paralled outside of the Arachnida, and it is not impossible that they may belong there. The appendages are easily homologised in the two groups, and especially interesting is the fact that while most genera in the female retain a primitive condition in having the genital ducts open upon several pairs of appendages (IV–VII), in a few these openings occur only on the seventh appendage, exactly where they occur in the Scorpions.

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II—LINGUATULINA.[17]

These forms, frequently associated with the Arachnids, possess but few points of similarity with them. Chief among these are the concentration of the nervous centres to a circumœsophageal ring, and the peculiar arrangement of the ovarian follicles. On the other hand, neither embryos nor adult resemble any Arachnids in more than a few superficial features. The opening of the genital ducts in the female near the posterior end of the body is not Arachnid in character, nor is the absence of "liver" lobes from the mid-gut. Besides, as non-Arthropodan characters, may be mentioned the extensive cœlom and the outer circular body muscles. The species of Pentastomæ have been so modified by parasitism that it is difficult to say whether the lack of other structures characteristic of Arthropods is due to primitive simplicity or to degeneration.

III—PAUROPODA.

The position of the Pauropoda is, as yet, very uncertain, as we are almost entirely ignorant of their internal structure. In the tendency towards a fusion of somites, in the lack of a second pair of maxillæ, and in the positions of the external paired openings of the genital ducts at the base of the second pair of ambulatory appendages and the non-motile spermatozoa they show undoubted affinities with the Diplopoda; but the peculiar triramous antennæ and especially the characters of the hexapod young, as figured by Lubbock ('67) and Ryder ('79) show important differences. The following table compares the somites of Pauropus and the Diplopod:

	DIPLOPOD.	PAUROPOD.
Appendage I	Antenna	Antenna
" II	Mandible	Mandible
" III	Lower Lip	Lower Lip
" IV	Foot 1	Absent
" V	Absent	Foot 1
" VI	Foot 2	Foot 2
" VII	Foot 3	Foot 3

[17] Upon points of structure and development consult Stiles ('91) and Spencer ('92), in addition to the older literature.

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IV—TARDIGRADA.

Elongate metameric animals with four pairs of appendages, each terminating with two double hooks. Mouth and anus terminal, Malpighian tubes present, opening into the hind-gut. Nervous system consisting of a supraœsophageal brain and a chain of four ventral ganglia. No specialised circulatory or respiratory organs. No coxal glands or nephridia. Sexes separate, gonad unpaired, emptying into hind-gut.

Most frequently the Tardigrades are associated with the Arachnida, but this has doubtless been due to the possession of four pairs of functional legs in the two groups. These forms differ from the Arachnids in the absence of all mouth parts,[18] in the proctodeal excretory tubes, the simple nervous system, smooth muscular tissue, and in the absence of nephridia, and they further differ from not only the Arachnids, but from all Arthropods in the fact that the gonads open into the hind-gut.

V—MALACOPODA.[19]

The Arthropodan features of the Malacopoda, represented by the single genus Peripatus, are the tracheæ, the legs terminating in claws, the appendicular nature of the jaws, the exclusive use of a pair of nephridia for genital ducts, the reduced cœlom; the several ostia of the heart, the heart being enclosed in a pericardium; the lacunar circulation. On the other hand, the Malacopoda differ from all other Arthropoda and agree with the Annelids in the following particulars:

The presence of functional nephridia in each body segment; the presence of well-developed coxal glands; the existence of an outer circular muscular layer in the body wall; the absence of striation from all muscles except those of the mouth parts; the presence of cilia in the alimentary canal and in the nephridia; the situation of the antennæ as outgrowths from

[18] The internal acicular teeth can hardly be regarded as appendages.

[19] I prefer to use the term Malacopoda for this group, because it is the oldest, being given by Blanchard in 1847. Onychophora of Grube dates from 1853, Protracheata was given by Mosely in 1874. The failure of Blanchard to recognize all points of structure does not invalidate his name.

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the primitively preoral region; the muscular nature of the pharynx, unlike that of any Arthropod and strikingly that of certain Chætopods. The eyes are too unlike the usual organs of any other Arthropod, but, as figured by Balfour, they closely resemble these organs in Autolytus. There is, too, an absence of a well-developed external cuticular skeleton, so that the absence of a true jointing in the appendages is noticeable. Judging from figures, the terminal claws of the legs might be compared with the setæ of the annelid parapodium.

On the whole, Peripatus cannot be placed beyond question in the Arthropodan phylum, and it is doubtful if it would have been placed there were it not for the presence of tracheæ. As we have already pointed out the existence of three different kinds of tracheæ which cannot be traced to a common origin, it is barely possible that those of Peripatus and the other "Tracheates" are not strictly homologous.

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TUFTS COLLEGE STUDIES, NO. II.

DEVELOPMENT OF THE LUNGS OF SPIDERS. By
ORVILLE L. SIMMONS.

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TUFTS COLLEGE STUDIES, NO. II.

DEVELOPMENT OF THE LUNGS OF SPIDERS.[1]

By Orville L. Simmons.

HISTORICAL.

Although several persons[2] had suggested the close affinity of the Arachnids and Limulus, it was not until the appearance of Lankester's paper, "Limulus an Arachnid" ('81) that the view of such a relationship came into prominence. Since that date it has attracted more and more numerous advocates until now the majority of the special students of Arachnids and Xiphosures recognize the close relationships of the two groups. One of the special homologies insisted upon by Lankester was that existing between the lungs of the Arachnids and the gills of Limulus. But to explain the difference between these organs—the one being an internal air breathing structure, the other an external apparatus for aquatic respiration—several hypotheses have been advanced, all based upon conditions existing in the adult.

At first, Lankester evidently shared the common view that tracheæ were homologous structures throughout the animal kingdom, and so he sought for traces of them in Limulus. In his article "On Stigmata in the King Crab" ('81[a]) he announced that he had found traces of stigmata. The position of insertion of each thoracico-abdominal muscle is marked by a deep funnel-like depression of the integument, which, from the external surface, appears as a stigma.

Later, in his paper "Limulus an Arachnid" ('81[b]), he formulates an hypothesis to show how the gills of Limulus and the lungs of Scorpio (taken because more primitive than

[1] Reprinted from the American Journal of Science and Art, III Series, Vol. xlviii, 1894.

[2] Strauss-Durckheim (teste Lankester), van Beneden ('70)

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Spiders) could have been derived from a common ancestor, which he describes as being an aquatic form, breathing by book-like gills. To derive Limulus from such a form would involve only a few changes in dimensions and other unimportant points. To obtain the condition occurring in Scorpio, assumes that the cup-like depression behind the appendages, as seen in Thelyphonus, became deeper and larger, finally engulfing the whole appendage. The walls then gradually extended over the cavity, leaving only a slit for communication with the exterior. As change of habits went on, this slit was closed up, and another slit, still within the area formed by the closure of the primitive opening of the cave of invagination, was formed. Air would enter by this slit, where in Limulus and the early Scorpion ancestors, there was a blood space. Thus a blood space has been changed to an air space. In the same way an air space (that of the investing sac) has been converted into a blood space. The atropy of the muscles which move the gills in Limulus and similar forms was considered very essential to this theory. The difficulties involved in the changes of blood and air spaces were so considerable as to prevent the acceptance of this hypothesis.

Later, Lankester ('85) puts forth a new theory. Because of discoveries concerning the muscles (veno-pericardiac) of Scorpio, as well as on account of the insuperable difficulties of his previous view, he gave up his old and advanced a new hypothesis. In the latter, the common ancestor is assumed to have had six pairs of mesosomatic appendages, of which five were lamelligerous. These latter in Scorpio became smaller and served only for respiratory organs, soon becoming air breathing. The four hinder pairs took a "trick" of growth, viz.: an invagination of the appendages, beginning at their distal ends, so that they grew into the Scorpion's body, turning their outside in, just as a glove may be turned wrongside out, beginning at the ends of the fingers. Thus the appendages would be tucked into the blood sinus instead of growing out normally. The blood sinus would become a venous sac around the appendage. He explains the "trick" of growth by the least resistance theory—the pressure being exerted on the embryo before it leaves the mother.

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J. MacLeod ('82 and '84) sets forth an hypothesis by which he develops Scorpions and similar forms from a Limulus-like ancestor. His first proposition is that the abdomen of Limulus be considerably elongated without other change. This would cause the imbrication of the members to cease—each appendage would stand out by itself, although closely following each other. Then suppose that the sternal plate increase in size and unite with the ventral surface of the abdomen. Thus the gill-book cavity would be entirely filled up by the sternal plate except in those cavities on the ventral side which contain the gills or lungs, now greatly reduced in size. In this condition the lungs are quadrangular plates, attached by two edges only. Inserted on each plate is a number of lamellæ which are attached by one side only. In this condition, when removed from the water, the lamellæ would cling together and be imperfectly in contact with the air. To be of service the lamellæ would have to unite their lateral edges to the plate, leaving only the posterior edge free. Thus MacLeod developed the lamellæ and other structures of the lungs of Arachnida.

By a comparison of structures in the adult form, MacLeod came to the conclusion that the trachæ of Spiders are developed from the lungs.

J. S. Kingsley ('85 and '93) advances a much simpler explanation to account for the transition from a Limulus gill-book to the lung-book of a spider or scorpion. By a sinking in of the whole appendage bearing the gill-leaves, and an increase of the inpushings of the integument and a decrease in the outgrowths, the whole matter is explained. This involves a diminution of growth on the anterior side of the appendage and an increase of growth on the posterior side. These conditions would carry the appendage within the body wall where it would be situated as seen in the adult—the spiracle at the posterior end of the lung cavity and the lamellæ projecting toward the posterior end of the body. As Kingsley states, viewed from a histological standpoint, the descript on of the pulmonary organ of the spider or scorpion applies, almost word for word, to the gill-book of Limulus. He believes that

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the lungs of spiders are the primitive and the tracheæ the derived structures. The tracheæ of the Hexapoda have no relation to the tracheæ of spiders, having an entirely different origin.

Malcolm Laurie ('90), in his article on "The Embryology of a Scorpion," thinks the lung-books are undoubtedly comparable to the abdominal appendages of Limulus, but hesitates to decide which of two propositions he advances is the correct one. He inclines toward the view that the lung-books of Scorpions are invaginated, i. e., the edge of each lamella in the Limulus gill-book corresponds to the interior fold between the lamellæ in the Scorpion lung-book. He imagines that he sees difficulties in explaining his second proposition, which states that the whole appendage has sunk without invagination into a cavity in the abdominal surface. By either proposition the air-space of the primitive condition would be air space in the derived condition.

On the other hand, many comparative anatomists, recognizing the homologies pointed out years ago by Leuckart as existing between the lungs and tracheæ of spiders, and believing that these last were the homologues of the structures known by the same name in the Hexapods, have failed to recognize the cogency of the reasoning of the advocates of the Arachnidian affinities of Limulus. Thus Arnold Lang, in his Lehrbuch der vergleichenden Anatomie (II Heft, p. 548, 1890), writes that the respiratory organs of Arachnoidea are tracheæ —tubular and book-leaf tracheæ. His view of the morphological signification of the latter is that they are modified tracheal tufts which, standing close together, have been flattened into hollow plates. He believes that the view of those who would bring the gill-books of Limulus and the lung-books of scorpions and similar types into close relationship, is artificial and unsupported by comparative anatomy and ontogeny.

So, too, Bernard ('92) in "The Apodidæ," says it is easiest to believe that the lung-books of the various forms are only a specially concentrated arrangement of tracheal tubes. He regards the tracheæ, including the lungs of all "Tracheates," as having their origin in dermal glands which have gradually

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been modified for respiratory purposes. He also states that in considering the relationships of these various forms, the limbs are of so little importance that one might almost be tempted to leave them out of account. In a latter paper on "The Chernetidæ," Bernard, ('93) repeats in substance his earlier views.

In a word, these authors, regarding the tracheal form of respiration as the primitive—a premise which the observations of Moseley on the tracheæ of Peripatus seemed to render valid—have looked upon the air tubes of the Arachnids as the primitive and the lungs as the derivative condition.

The question thus brought into prominence can only be settled by tracing the development of the respiratory organs of the Arachnida. Several authors have touched upon this question. Thus Locy ('86) describes the later stages of *Agelena nævia* as follows: The lungs arise as a pair of extensive invaginations. In sagittal sections they appear as oblong plates of cells with the nuclei in parallel rows. These nuclei are flattened on one side and convex on the other. The cells of two adjoining rows unite by the edges toward which the convex sides of the nuclei project, and thus a lamella is formed. Later the nuclei of adjoining cells fuse, forming protoplasmic pillars between which are the blood lacunæ. Around each lamella is a chitinous membrane—the ventral and the dorsal being continuous at the free (posterior) end of the lamella. The cells of the ventral wall become arranged into two distinct layers. A part of the development described takes place after the hatching of the egg.

A. T. Bruce ('86 and '87) says that a lung-book of a spider may be regarded as an involuted appendage or appendages. He noticed that the abdominal appendages become less conspicuous, and that slight folds appear on their *anterior* faces. He did not observe all the stages, and, judging from his text and figures, it is very evident that he was confused in some of his interpretations. K. Kishinouye ('90) states that in the basal part of the first abdominal appendage there is an ectodermic invagination—not deep or large. The wall of this pocket which faces the distal end of the appendage is thicker,

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and its cells become arranged in parallel rows. Two of these rows, adhering to each other, produce a lamella. He confirms Locy's description of the later stages. On the second abdominal appendage is another ectodermic invagination—a deeply invaginated tube which remains in about the same state of development until after hatching. The appendage shortens, but is not invaginated. He believes it is very probable that the lungs were derived from the respiratory apparatus of some Limulus-like aquatic form. He thinks that tracheæ are modified lungs.

Laurie ('90), beginning with his stage K, describes the changes in the abdominal segments of the Scorpion. At this stage the pectines and lung-book appendages are about equal in size and structure. In stage L, the pectines have become folded in a direction transverse to their axis. The other appendages are pushed in, forming little cavities (directed forward) on the posterior side of the appendages. In the stage *M* the pectines are separated from the body wall at their distal ends. The lung-book inpushings are deeper and the cavities are divided up by lamellæ. In the last stage described (just before hatching) the pectines and lung-books have much the same structure as in the adult.

Morin ('88[3]) states that the lungs of the dipneumonous spiders arise in form of infoldings at the bases of the two appendages of the second abdominal segment. At the anterior end of the sac on the dorsal side, is an infolding which is the beginning of the lung leaves. The space between two leaves connects directly with the body cavity. Two adjoining leaves unite by the fusing of nuclei, as described by Locy. He agrees with Locy as to the later stages. Morphologically, the lungs of Arachnida show great resemblance to the gills of Limulus and similar forms. He emphasizes the position of the infoldings on the posterior side of the appendage in both cases. The lungs of spiders are merely sunken gill-books of Limulus. As the appendage sinks, the stigma is left as an opening between the posterior wall of the appendage and the

[3]As summarized by Korschelt and Heider, '92, pp. 604-607. I cannot refer to the original Russian text.

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body wall. This author agrees with those who believe that tracheæ are modified lungs.

It must not be forgotten that Elias Metschnikoff ('70) described some features of the lungs of the Scorpions, but it is not easy to understand either his text or his figures beyond the fact that he states that the lungs develop behind the abdominal limbs.

INVESTIGATIONS.

As will be seen from the foregoing summary, the development of the respiratory organs of the Arachnids has not been followed throughout, and the gaps in our knowledge are at just the most critical points. To supply these deficiencies the investigations described below were undertaken.

The work was done in the Biological Laboratory of Tufts College. The eggs used were those of *Agelena nævia* and *Theridium tepidariorum*. The eggs were killed in water heated to 80° C., and hardened in alcohol, beginning with 50 per cent. The staining was usually *in toto* with alum cochineal. The sections described, unless otherwise specified, are sagittal.

In the first stage studied, corresponding in general to Locy's fig. 6, the somite VII is cut off from somite VIII. Somites VIII and IX are still united (fig. 1) and the unsegmented mesoderm extends further back. The ectoderm is a single layer deep, excepting a portion over somite VII (possibly the anlage of an appendage) and between VIII and IX. The infolding of ectoderm shows the first differentiation of external segmentation.

In the next stage (fig. 2) which is about midway between Locy's figures 6 and 7, the second abdominal somite is differentiated, and to a less extent the line between somite IX and somite X, which has developed, is marked off. The ectoderm has become thickened from somite VII to somite IX. It is to be noticed that the cœlomic pouches are flattened in all except somite VIII.

The succeeding stage (fig. 3) shows the same features carried still farther. The XI somite has appeared. This stage corresponds to Locy's figure 7 or a stage a little earlier. I may note here that I have found at least as many cœlomic pouches as

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are described by Kishinouye in "Note on the Coelomic Cavity of the Spider," 1894.

After the stage just mentioned, the appendages begin to be formed; no detailed account need be given of the external appearance of these, as in the main, my observations are but the repetition of those of various authors, from Claparède to Kishinouye. They grow out, one on either side of somites VIII–X, as rounded knobs.

PULMONARY ORGANS.

In figure 4, which represents somites VII and VIII, the early appearance of the appendage is seen. In somite VII the cœlomic is already greatly reduced and no trace of an appendage is to be seen. In the next somite (VIII) the appendage is plainly visible. It is marked off from somite VII by a slight groove, while the groove separating it from somite IX is deeper and directed forward, giving the limb a markedly backward direction, a tendency which is even more pronounced in later stages. Its outer wall is formed of several layers of cells, while the cœlomic pouch sends into the budding appendage an outgrowth like that described by various authors.

With farther growth the conditions just described become more strongly emphasized; the anterior demarkation of the appendage becomes more and more faint, while behind, the inpushing becomes more and more marked, so that eventually a pit is formed, actually extending into the general body surface, the outer wall of the pit being formed by the appendage whose growth we are tracing. This pit forms the pulmonary sac and the opening of the inpushing persists as the respiratory stigma. At no time do the appendages rise to any considerable distance above the general abdominal surface.

The changes described can be seen by a glance at fig. 5, which, besides the points already mentioned, shows some other features worthy of notice. The cœlome of somite VII still persists. That of VIII has become divided into two portions, one of which remains in the appendage, while the other portion, reduced in size, has been pushed backward by the ingrowing pulmonary sac. The sac itself is irregular in outline, its

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inner wall being slightly undulating, while its outer wall, *i. e.*, the morphologically posterior surface of the appendage, has its ectoderm thrown into folds, the anlagen of the leaves of the lung-book. The ectoderm lining the inner wall of this sac is but a single cell in thickness, but that of the appendicular side is thicker, the nuclei being rather irregularly arranged, and the pulmonary ingrowths forcing their way between them. In this stage but two lung leaves are outlined, as shown in the figure.

In eggs of the same lot as the last, a stage apparently a little older was found; and from it the section figured in 6 was drawn. In its general features the changes are slight, but there are some details of importance. From the fact that the plane of this section is not the same as that of the last, the appendicular cœlome is not shown, while the cœlomic cavity of the body is here much larger. So, too, the inner wall of the pulmonary cavity is shown to be thicker, a fact probably due to the obliquity of the section. In this stage four gill leaves are shown, the most developed ones being the most distal ones. In these, too, the nuclei are already arranged with their major axes parallel to the plane of the leaves. Proximally the leaves are much shorter and the nuclei are irregularly arranged. These facts place it beyond a doubt that the growing point of the organ is at the base of the appendage, a point of no little importance in comparison with the Xiphosures.

Figure 10 shows the ventral view of the embryo at the stage which figures 5, 6 and 8 represent in sections. This stage is about two or three days before the reversion of the embryo. Changes during this period are very rapid. In 4–5 days after this stage the lungs are almost fully developed, and have about the same appearance as in hatched specimens, except in size and number of lamellæ. The embryo hatches in from 7–8 days after the stage figured in 10.

With the reversion of the embryo, the changes rapidly proceed toward the adult condition. In fig. 7 I insert an illustration which serves to connect my account with the papers of Locy, Kishinouye, Laurie and others. Here the gill lamellæ have slightly increased in number, while they have become

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greatly increased in length. In the figure the pulmonary sac is somewhat funnel-shaped, owing to a pulling open of the spiracle in some process of manipulation.

From this stage the transition to the conditions described by MacLeod and Locy are but slight, and although I have studied the later stages up to and even beyond hatching, my observations are but a confirmation of theirs, and so I do not repeat them here. The lungs are well-developed and apparently ready to function as respiratory organs at the time of hatching. With the growth of the young spider the principal changes are an increase in the number of lamellæ and a corresponding increase in the size of the pulmonary organ, the new lamellæ being formed at the inner end of the sac.

TRACHEÆ.

The study of these has been a matter of considerable difficulty, and I have been able to follow with certainty only the earlier stages. The tracheæ arise behind the appendage on somite IX, which, in its earlier stages, has exactly the same history as appendage VIII. There is the same inpushing behind the limb which results in its taking a position not pointing outward, but toward the median line and backward. In fig. 8 is seen the first differentiation of the tracheæ. The inpushing has given rise to the spiracle as before, but the sac which results does not show so markedly those infoldings of the appendicular wall which occur in the case of the lungs. There is, at most, but a slight undulation of this surface. At the inner end, however, two ingrowths are seen, the earliest indications of the formation of the tracheal twigs. It is, however, easy to see that these inpushings are to be compared with the infoldings which produce the lamellæ, while the undulations just referred to admit of the interpretation that they are aborted gill leaves.

After the reversion of the embryo, the same parts can be recognized (fig. 9). The inpushing has been carried to a greater extent, and sections in other planes show that this ingrowth is tubular in character. The cells lining its walls are elongate, and are already taking the character shown in the

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tracheæ of the adult. At the inner end of the tracheal trunk thus formed, the nuclei are arranged in a radiating or bush-like manner, apparently indicating that here is the place where the trunk is about to divide into the tracheal twigs, but I have not been able to trace any tracheal lumina between these cells. I have not followed the later history of the tracheal system with any detail, but think that the foregoing is sufficient to justify my thesis that the tracheæ and the lungs are to be regarded as homologous structures.

CONCLUSIONS.

From the preceding it will be seen that:

I. The lungs of the spider arise as infoldings upon the posterior surface of the appendages of the second abdominal somite in the same manner as described by Kingsley ('85 and '93) for the gills of Limulus. They have the same growing point at the base of the appendage, and form the lung leaves in exactly the same way that the gill-leaves arise. In other words, the lung-book of the spider (and presumably of all Arachnids which possess one) arises at first as an external structure upon the posterior surface of the abdominal appendages. These appendages sink in, without any inversion or other complications, in exactly the manner theoretically deemed probable by Kingsley, so that there can no longer be any doubt as to the exact homology existing between the lungs of the spider and the first pair of gills in the horse-shoe crab.

II. The tracheæ develop from the next pair (third abdominal somite) of limbs. In their earlier stages these appendages show on their posterior surface a folding similar to that on the preceding members. From this it follows that the lung-book condition is the primitive, the tracheæ of the Arachnids being derived from it. And with these facts there is left no ground for those who regard the "Tracheata" as a natural group of the animal kingdom.

Tufts College, Mass., May 25, 1894.

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EXPLANATION OF THE FIGURES.

REFERENCE LETTERS.

a^1.–a^{11}. Appendages.
c^7.–c^{11}. Coelomic cavities.
e. Ectoderm.
m. Mesoderm.
pc. Pulmonary cavity.
pl. Pulmonary leaves.
s. Spiracle.
so. Somatoplure.
sp. Splanchnoplure.
t. Trachea.
y. Yolk.

All figures, except fig. 10, are magnified 125 diameters.

EXPLANATION OF THE PLATE.

FIG. 1.—A sagittal section showing the cœlomic cavities of the VII, VIII and IX somites.

FIG. 2.—A sagittal section through the same region as the preceding at a little later stage. The cœlomic pouch of the X somite is seen, as well as the inpushings of ectoderm behind somites VII and VIII.

FIG. 3.—A section cut under conditions similar to those of the two preceding. The stage is a little later than fig. 2, and shows the cœlomic cavity of somite XI aud further inpushings of the ectoderm. In all of the preceding sections the somatopluric wall is the thicker.

FIG. 4.—In this figure the cœlome of somite VII is much reduced in size. The cœlome of VII is beginning to thrust itself into the appendage which is marked off by a shallow groove in front and by a deeper inpushing, which has a forward direction, between somites VIII and IX.

FIG. 5.—In this section the inpushing, seen in fig. 4, has gone much farther, dividing the cœlome of somite VIII into two parts. On the inner wall of the appendage are two inpushings which are the beginning of the lamellæ of the lung book.

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FIG. 6.—A section of the appendage of somite VIII cut at a different angle from the preceding. Here four lamellæ are seen.

FIG. 7.—A sagittal section from a stage just after the reversion of the embryo.

FIG. 8.—A section of the appendage of the IX somite, showing at the inner end of the inpushing, the beginning of the tracheal tubes.

FIG. 9.—This is a section of the tracheal region after the reversion of the embryo.

FIG. 10.—This figure is a representation of the ventral surface of an embryo, which is about the same age as those from which sections seen in figs. 5, 6 and 8 were cut.

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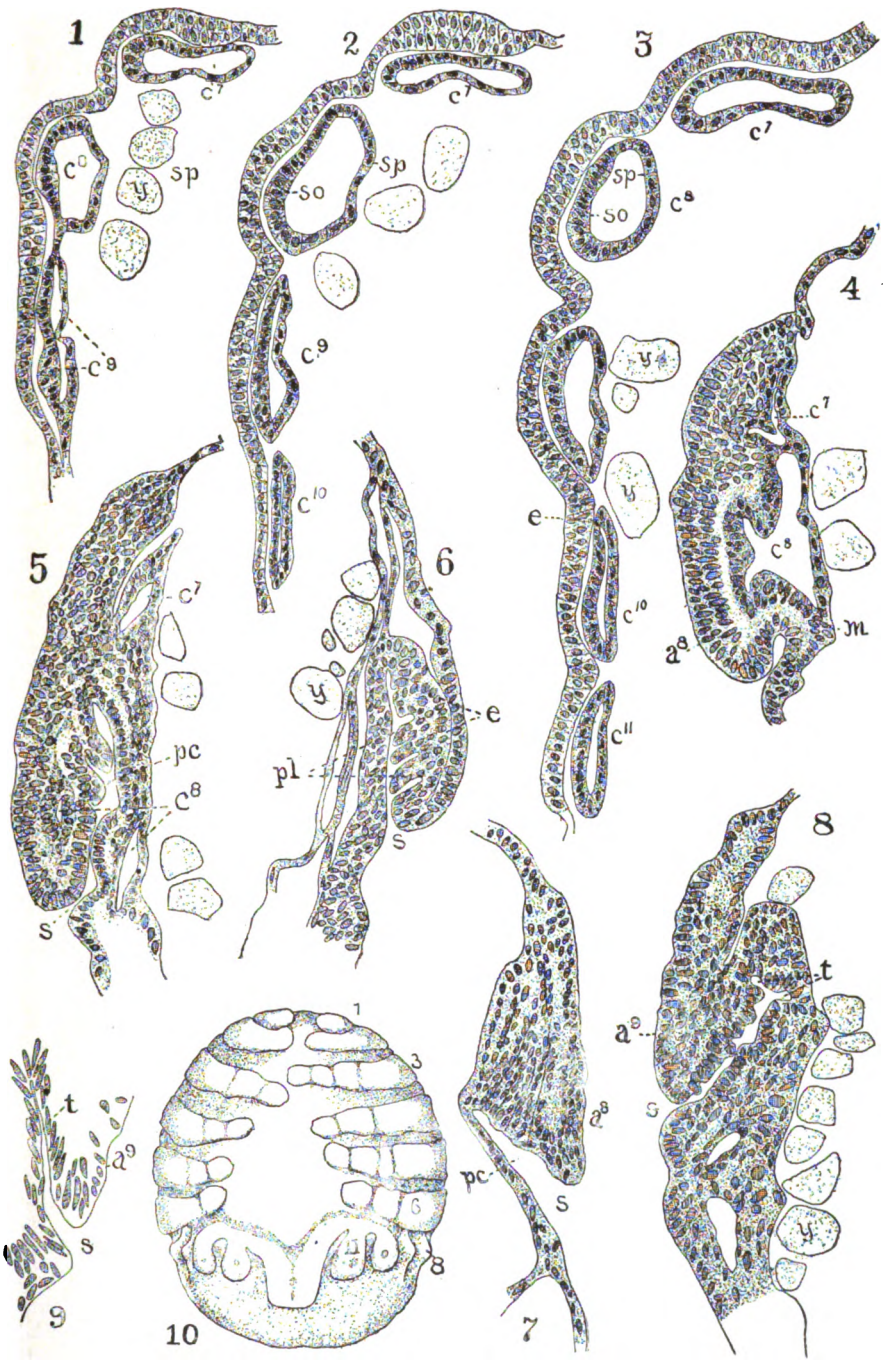

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Published by the Charles Hyde Olmstead Fund.

TUFTS COLLEGE, MASS.
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TUFTS COLLEGE STUDIES, NO. III.

THE DEVELOPMENT OF THE WING OF STERNA WILSONII.[1]

By Virgil L. Leighton.

Although various students have investigated the structure and the development of the wing of the bird, many points still remain unsettled, and prominent among them, the relations of the carpal elements, the number of digits present and the comparison of these digits with those of the normal pentadactyl manus. Professor J. S. Kingsley suggested to me to attempt the solution of some of these problems, and the studies detailed below were carried out in the Biological Laboratory of Tufts College under his direction. To him I owe the material—embryos of various stages of Wilson's tern, *Sterna wilsonii* from the Island of Penekese, Mass.—which formed the basis of my work.

The alcoholic material was studied both in toto by clearing with oil of clove, and by means of serial sections. The latter proved far preferable and much more dependence can be placed upon results obtained in this way, especially with the younger embryos than by the more common methods of dissection and clearing in essential oils. The figures of structural details which illustrate the paper were obtained from reconstruction projections of the sections and are magnified twenty diameters. I am not able to state the ages of the various embryos, but this is a matter of little importance since the approximate development can readily be made out from the figures of the various stages, each natural size. The numbering of the separate stages is entirely arbitrary.

I might state here, incidentally, that I have also studied to some extent the foot of the tern and I find in it, as has already been pointed out by other observers, (Miss Johnson, Studer, W. K. Parker and others) a fifth metatarsal present.

[1]Reprinted from The American Naturalist, Vol. xxviii, p. 761, 1894.

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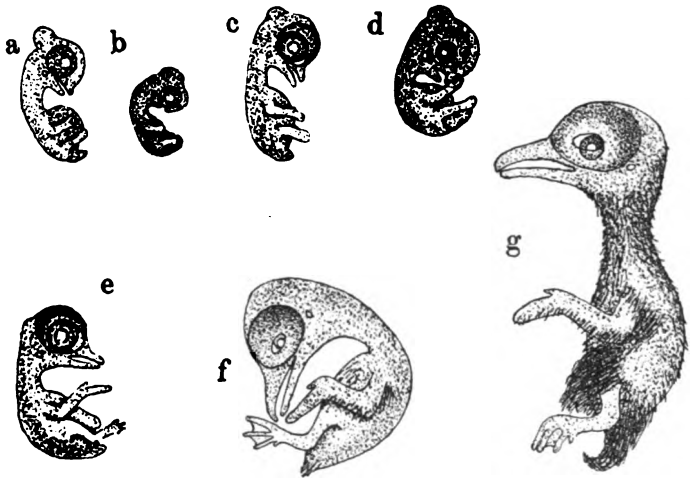
STAGE I, (FIG. 1).

At this stage (fig. a) the principal elements of the wing are becoming differentiated. The radius and ulna are entirely cartilaginous, except a small portion at their distal ends where they are least developed. In the proximal row of carpals are two masses of rapidly forming cartilage (radiale and ulnare) each of which appears to have two centres of chondrification.



The larger (the radiale, *re*) is almost divided into two parts; of these the larger and outer one is somewhat triangular in shape and is fitted upon the distal end of the radius, the smaller and inner one is nearly circular and is contiguous to the inner margin of the distal end of the ulna. The ulnare is composed of two oval centres, the proximal being about half the diameter of the distal one, thus giving the whole element a wedge-shaped appearance with its narrow end passing just outside the outer margin of the ulna.

The distal carpals are represented only by a thickening of tissue, or "procartilage" of Parker, showing as yet no differentiation into separate elements. There are *four* radiating digits represented for the most part by "procartilage," but metacarpals II[1] and IV are becoming cartilaginous at their proximal ends and metacarpal III is two-thirds cartilage.

[1]For the numbers to be given to the digits, see below.

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STAGE II, (FIG. 2).

This stage (fig. b) is but slightly more developed than the last. The cartilage is a little more pronounced, and digits II, III and IV have become longer, III and IV being segmented. The fourth digit has become free from the central mass, and more nearly approximated to digit IV. In the distal carpal series there are two masses of cartilage: on the radial side a mass which represents the combined carpales II and III, and on the side of the ulna carpale IV, an oval mass contiguous proximally to the distal lobe of the ulnare and distally to its own metacarpal.

STAGE III, (FIG. 3).

In this stage (fig. c) there are several things to be noted. The spreading of the digits is not so great and the whole manus is beginning to flex towards the ulnar side, thereby displacing some of the carpals from their normal position. The elements are now all perfectly distinct, the radiale has entirely lost its bibobate appearance, and is now of an irregular shape, touching the radius and ulna and the approximate surface of the conjoined carpales II and III. The ulnare is now entirely outside the ulna, but, what seems most remarkable, its proximal portion is now about twice the size of its distal lobe, while in the stages previously described it is about half as large. The distal lobe is circular, the proximal wedge-shaped, with the small end proximal. Carpale II+III is the last carpale to chondrify, but is now all cartilage except a very small portion of its proximal end. It is an elongate mass, placed somewhat diagonally to the present axis of the limb. It is contiguous distally to the approximate surface of metacarpals II and III and carpale IV; proximally to the radiale. Carpale IV retains the same relative position as in earlier, except that it has approached closer to metacarpal III. Digits II and III have each added a segment, that of the former is partly cartilaginous, the latter is all procartilage. Metacarpal IV has approached metacarpal III and its single phalanx is entirely cartilaginous. Metacarpal V has the same appearance as in previous stages, but is farther from metacarpal IV.

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STAGE IV, (FIG. 4).

The specimen which forms the subject of this stage (fig. d) is in some respects slightly more developed than stage III, in other respects less so. The manus is not flexed so much, and consequently the ulnare has not been pushed so far outside the ulna. In this specimen, unlike the others, the two lobes of the ulnare are about equal in size, the distal one oval, the proximal wedge-shaped. The radiale retains its bilobate appearance as described in stage I. Carpale II+III forms a lunate mass of fully developed cartilage about the head of metacarpal III. Carpale IV is slightly smaller relatively than in the previous stage; the digits are essentially the same.

STAGE V, (FIG. 5).

In the specimens (fig. e) which forms the basis of this stage, the manus now assumes very nearly the form which it has in the adult bird. The radiale is irregular in shape and fitted to the distal end of the radius, the inner distale margin of the ulna and the approximate surface of carpal II+III. The distal lobe of the ulnare is here at a minimum in comparison with the proximal lobe; it is now closely appressed to carpale IV which is wedged between it and carpale III. Metacarpal II has approached metacarpale III and on its radial side is developed a large projection or "trochanter." Its proximal phalanx is entirely cartilaginous, its distal one is just beginning to appear. Metacarpal III now bears three phalanges, the distal one not yet cartilaginous. Metacarpal IV has assumed a position parallel to metacarpal III, but is not yet united to it. Metacarpal V has approached metacarpal IV near its proximal end.

STAGE VI, (FIG. 6).

In birds of this age (fig. f), carpales II, III and IV have entirely coalesced, and, together with metacarpal II, form a solid socket into which fits the head of metacarpal III. Metacarpal II bears two phalanges; metacarpal III three, their distal phalanges being unequal. Metacarpal V now touches metacarpal IV and is not so near the proximal end as in earlier stages.

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STAGE VII, (FIG. 7).

There is little in this stage (fig. g) to note except metacarpal V. This is now an oval disk closely applied to the ulnar flexor surface of metacarpal IV, about one-ninth of the distance from the proximal to the distal end. It no doubt finally unites with metacarpal IV at that point.

COMPARISONS.

INTERMEDIO-RADIALE. In Sterna in the earlier stages these two elements are distinct (fig. 1); later they become so completely fused that they cannot be distinguished, although, exceptionally, (fig. 4) they partially retain their individuality for a considerable time. Similar conditions have been noted in several birds, *e. g.*, Opisthocomus, *Falco tinnunculus* and chick by Parker and *Cypselus melba* by Zehntner ('90). In other birds the separation has not been described, possibly from the fact that the proper stages have not been studied.

ULNARE-CENTRALE. My observations here closely agree with those of Parker on the ducks and auks, there being the same tendency to subdivision of the cartilage mass into two elements which he shows. One of these is, beyond doubt the ulnare, but I confess I am not so certain of the other which I call centrale in deference to his better opinions. The conditions shown in fig. 1 where the two portions of this element are clearly shown, leads one to the conclusion that the distal lobe may possibly belong to the series of carpales, in which case it would be that of the fourth existing digit. In fig. 5 again the arrangement is such as to support such a view, while on the other hand, in none of the earlier specimens have I seen it in such a position as to indicate that it should be regarded as a centrale. In *Chloëphaga poliocephala* Parker ('90) describes this bone as divided into three portions, the two distal of which he terms centrale 1 and 2. It would rather seem as if we had here to do with a true centrale, while Parker's centrale 1—clearly, according to position, equivalent to the single one which I find—must be regarded as a fourth carpal. (Cf. Parker '90, pl. 5, fig. 14). Studer, according to the

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single figure copied by Wiedersheim, has different ideas. He has no such projection from the ulnare, but in his figure carpale I+II projects up between radiale and ulnare and the projecting portion is the centrale. Zehntner, on the other hand, ('90) has the intermedium united to the ulnare, the centrale to the radiale, conditions which certainly do not occur in Sterna.

CARPALS. Unless we regard the "centrale" of the preceding paragraph as in reality a carpal, Sterna never possesses more than two distinct elements in the distal carpal series. Of these that on the radial side is the larger. When chondrification begins it occupies a position (fig. 2) at the base of metacarpal III; later (figs. 3, 4) it extends radially towards metacarpal II, and even at times (fig. 4) exhibits a marked bilobate appearance. From these facts as well as its subsequent history I regard it as a compound body, the carpales II+III of the normal pentadactyle hand, the distal carpal II of Parker and most other students of Avian osteology. Concerning the "pentosteon" of Shufeldt I can say little. This author ('82 p. 691, footnote) gives this name to a small bone found by him in Centrocercus lying at the base of the plantar surface of the second (my third) metacarpal. The name was given because it was the fifth carpal bone discovered, and because it was noncommittal as to its homologies. Parker now finds the same bone in ducks and auks, occupying the same position, and regards it as carpale I. This interpretation, however, seems to me faulty, as the bone is not in the proper position for such identification, nor have we any torsion or stress which could account for such translation. It would appear rather to belong to the same category as the pisiforme, but since I have not found it in Sterna I can offer no further observations upon it.

The other free carpal element, carpale IV, is clearly but a single element and not a compound structure like that described by Zehntner, Rosenberg and others. Studer, in the penguin, also figures a broad element in this position which he doubtfully regards as compound. In Sterna this element at its first differentiation is no wider than the fourth metacarpal, and as long as it retains its free condition it remains re-

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latively of the same size. Later (fig. 6) it becomes united with carpale II+III, the whole forming a single piece equivalent to the separate os magnum and unciforme of some birds.

METACARPALS. The only metacarpal which requires notice is V (IV of many authors). This has been more or less perfectly described by several students since its first discovery by Rosenberg ('73). This author describes it in the chick as a distal process of a common mass of cartilage which clearly contains *two* carpal elements, IV+V, since to it is also joined metacarpal IV. In the case of his figures there can be no doubt that this distal prolongation is a true digital element, as it is clearly homonomous with the other metacarpals. It is to be noted that according to Rosenberg this new metacarpal lies at a lower level than the others, being flexed towards the palmar surface. Zehntner ('90) finds the same element in *Cypselus melba*, but existing there, as in Sterna, as a piece distinct from the basal (carpal) element with which it is at first joined in the chick. According to Zehntner after 9 or 10 days, this metacarpal "geht.... bei Cypselus einen vollständigen Atrophie." This is certainly not the case in Sterna, nor is it in those forms studied by Parker. Here it retains its discrete nature for some time, and in the fowl, toucan and cariama it even becomes ossified before its final union with the basal end of metacarpal IV.

That this is a true metacarpal is, I think beyond question. Owing to the method of study adopted by Parker he failed to recognize its earlier conditions, and his observations, unsupported by other evidence might be interpreted, as has been done by several, in another way. However, the evidence adduced by Rosenberg, Zehntner and myself, clearly removes this from the category of tendinous ossifications, the pisiforme and the like.

Naturally the structures which I have described should be compared with those of the reptiles, but this to be at all adequate would require a detailed knowledge far greater than I possess. It is to be noted, however, that if, as contended in the next section, the avian "pollex" is not the first digit of the pentadactyle hand, a portion of the reasons adduced for

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regarding the Pterodactyls as widely removed from the birds is removed.

THE HOMOLOGIES OF THE DIGITS.

In the wing of the adult bird only three digits at most attain full development, and, since the birds have descended from pentadactyle forms, it becomes a matter of some importance to compare these three with those of the normal hand; in other words to ascertain which digits have been lost in the process of evolution. Naturally many attempts have been made to solve the problems involved, and within the last decade four different views have had their advocates, though naturally some of these ideas of homology date back to a more remote period.

Thus Gegenbaur ('64), reasoning from the apparent tendency towards reduction of the digital elements on the ulnar side of the crocodilian manus, concludes that the persistent digits of the bird wing are the I, II and III of the normal pentadactyle hand. In this he has had many followers, among them Rosenberg ('73), Huxley ('71), Jeffries ('81), Jackson ('88), and Parker ('88). For this view there are many more arguments than the one mentioned above, and Dr. Jeffries has given an able summary of them.

A second view is that of Owen, according to which the digits in question are II, III and IV. This is based partly ('36) on the fact of the absence of the radial artery, which would indicate reduction on the radial side of the manus; and partly ('62) on features supposed to exist in the British Museum specimen of Archæopteryx. In this there are apparently four digits present in connection with the right wing, but as these show considerable dislocation, one may, as suggested by Professor Owen, have belonged to the other side. This view has fewer supporters than the other, among them Morse and Coues. Morse ('72) contributes not a little in support by his advocacy of the law of digital reduction as a valid argument in this connection. That Coues supports the same view I take partly on the statement of others and partly from the fact that, while in the text of his "Key" ('87), he gives both views, the num-

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bering of the digits is II, III, IV. In an earlier paper ('66) he accepts the numbering I, II and III. Here, too, must be enumerated Shufeldt, who states ('82, p. 616) that he has always adhered to this view, but adds "the fact, however, that the first phalanx of the manus of aves is the homologue of the pollex of the pentadactyle limb seems to be gaining ground." I have not found any further reference to this subject in his subsequent osteological contributions further than this usual reference to the radial digit as the pollex.

Mr. Hurst ('93) has advocated a third system of numbering according to which the digits are III, IV and V. An analysis of his reasons will be given immediately when dealing with the arguments for the enumeration adopted in the present paper.

The fourth system is that of Tschan ('89) who according to Zehntner ('90) proposes to regard the permanent digits as I, II and IV. He bases this on the discovery by Parker ('89) of a slip of bone in chick,[2] Musicapa and many Gallinæ as occuring between the second and third of the persisting digits. This, says Tschan, is the true digit III. But Parker further describes similar slips as occurring on the outside of the "pollex" and between the first and second permanent digits as well as a true fourth metacarpal on the ulnar side of the hand. Tschan suggests that the first of these might be the "prepollex" but even with the admission of this doubtful element, there would be one superfluous digit. This together with the utterly anomalous type of reduction which it presupposes—the disappearance of digits in the middle of the manus—is sufficient to discredit this view.

That there is developed a fourth digit in the avian manus is beyond question, and the fact that this comes upon the ulnar side of the three permanent fingers is sufficient to invalidate the nomenclature, III, IV and V of Hurst. Hurst refers to Parker's fourth digit as appearing to be the *os pisiforme*, and since Parker had only the later stages, there would be some plausibility in this view. This possibility, however, disappears

[2]It was discovered, as Parker points out, long before by Heusinger ('20, pl. IV f. 10) in the chick, persisting for sometime as a separate bone.

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when we study not only my figures 1 and 2, but the figures of Rosenberg and Zehntner. In the figures just cited the temporary digit is just as prominent as is the "pollex" and no one without a theory to support would regard it other than a digit. Then too, as Rosenberg's figure shows, it bears no connection to the ulnare, but is a distinct outgrowth from the outer distal angle of carpal III+IV.

We are then left to choose between the formulæ I, II and III and II, III, IV, and though the apparent weight of authority is in the other direction, I am strongly inclined towards the second alternative, for the following reasons: First comes the law of digital reduction advocated by Morse, by which in other groups digit I is first to disappear and then V. Further, when further reduction occurs in birds, and a single digit is left, as in the Apteryx and the Cassowaries, the reduction has occurred on both sides of the persisting digit, which, according to my nomenclature, would be digit III. This implies a symmetrical reduction, the other view involves the disappearance of digits I, III, IV and V, a condition, so far as I am aware, without parallel.

Then too, Archaeopteryx, in the light of Hurst's later studies presents some evidence. As noted above, Owen thought he had found evidence of a true digit I in the British Museum specimen, but on the discovery of the Berlin specimen this idea was dropped and the conditions presented by the new example form the chief argument in Jeffries' summary already alluded to. It would, however, appear that most recent figures of the Berlin specimen and the conclusions based upon them are not to be relied upon. This can be at once seen by comparing for instance the figure of Archaeopteryx given by Zittel in his Paleontologie with the photographic reproduction which illustrates Hurst's article.[3] In the Berlin specimen three digits in the wing are clearly visible, and it has been assumed that these were the only ones. Hurst, however, points out that the position of the feathers is such that they could not have been borne on these digits as in ordinary birds,

[3]The plate in the Standard Natural History (Vol. IV, facing p. 22, 1885) approaches very closely the figure of Hurst.

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but that there must be (at least one) digits buried beneath the feathers, and in just the place where the missing finger or fingers should come is an evident ridge in the stone.

If we may call upon the effects of use and disuse, the conditions presented would also tend to favor the reduction of the digits on the radial side, for it is the ulnar phalanges which must bear the stress of the wing; the fingers on the radial side, having but few small feathers, would be most likely to disappear.

Jeffries invokes also the distribution of the nerves, but to my mind his evidence is not conclusive; besides it is directly negatived by the distribution of the blood vessels as was pointed out above.

We may conclude, then, that the only conditions possible are either I, II and III, or II, III and IV, and that until some evidence be found of the actual appearance of a fifth digit on the ulnar side, that there is at least as much reason for the second as for the first formula. In regard to the first, Hurst remarks, it "is in no case, so far as I am aware, supported by any evidence whatever. I believe it to have originated from the pre-Darwinian statement that the Ala spuria is 'analogous to the thumb;' while the other two digits are called simply 'second' and 'third;' that is, *second and third digits* not of the pentadactyle but *of the tridactyle fore-limb.* Such phrases written on the then undoubted hypothesis of special creation and of fixity of species, could obviously not mean that the three digits called 'thumb' and 'second' and 'third' had been evolved from the digits I, II, III of the pentadactyle fore-limb of an ancestor; the author did not believe that birds ever had such an ancestor. The transcription of such phrases into post-Darwinian treatises, without consideration of the new meaning which they would thus gain from the new context, appears to have been the origin of the error."

CONCLUSIONS.

CARPALS. There are at least seven elements in the carpus. In the proximal row there are two free elements (intermedio-radiale and centralo-ulnare) both of which are divided in the

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early embryo, and represent, morphologically, the radiale, intermedium, centrale and ulnare. In the distal series there are also two free elements, one of them (carpal II+III) being evidently compound.

DIGITS. There are four distinct metacarpals. The first (II) supports two phalanges, the second three, the third one, and the fourth none. The distal phalanges of m. c. II and III are furnished with claws. *M. C.* V arises as a distinct digit, subsequently becomes free, and finally unites with m. c. IV.

NUMBERING OF DIGITS. The persistent digits of the birds wing are either I, II and III or II, III and IV, the bulk of evidence being in favor of the latter enumeration.

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EXPLANATION OF THE FIGURES.

The illustrations in the text show the embryos natural size. It is to be noted that fig. A, showing a smaller embryo, had a wing more developed than fig. B. All other figures are projections of camera drawings and are each magnified 22 diameters.

REFERENCE LETTERS.

c carpale	*m. c.* metacarpal.
h humerus	*u* ulna.
r radius	*ue* ulnare.
re radiale	II–IV and I–IV digits.

Fig. 1. Manus, stage I, showing carpus and digits as procartilage with several cartilaginous elements. Digit V is plainly shown.

Fig. 2. Manus, stage II. Three carpals are now seen and metacarpal V has become distinct from the carpal mass.

Fig. 3. Manus, stage III. The digits are now broken into phalanges and the flexure of the hand to the ulnar side is forcing the ulnare out of its normal position.

Fig. 4. Manus, stage IV. The radiale shows tendency to division into radiale and intermedium.

Fig. 5. Manus, stage V. Elements now beginning to ossify. Digits II and III are terminated with claws.

Fig. 6. Carpals and metacarpals, stage VI. Carpals united; metacarpal V approximate to metacarpal IV.

Fig. 7. Conditions just before hatching. Metacarpal V joined to metacarpal IV.

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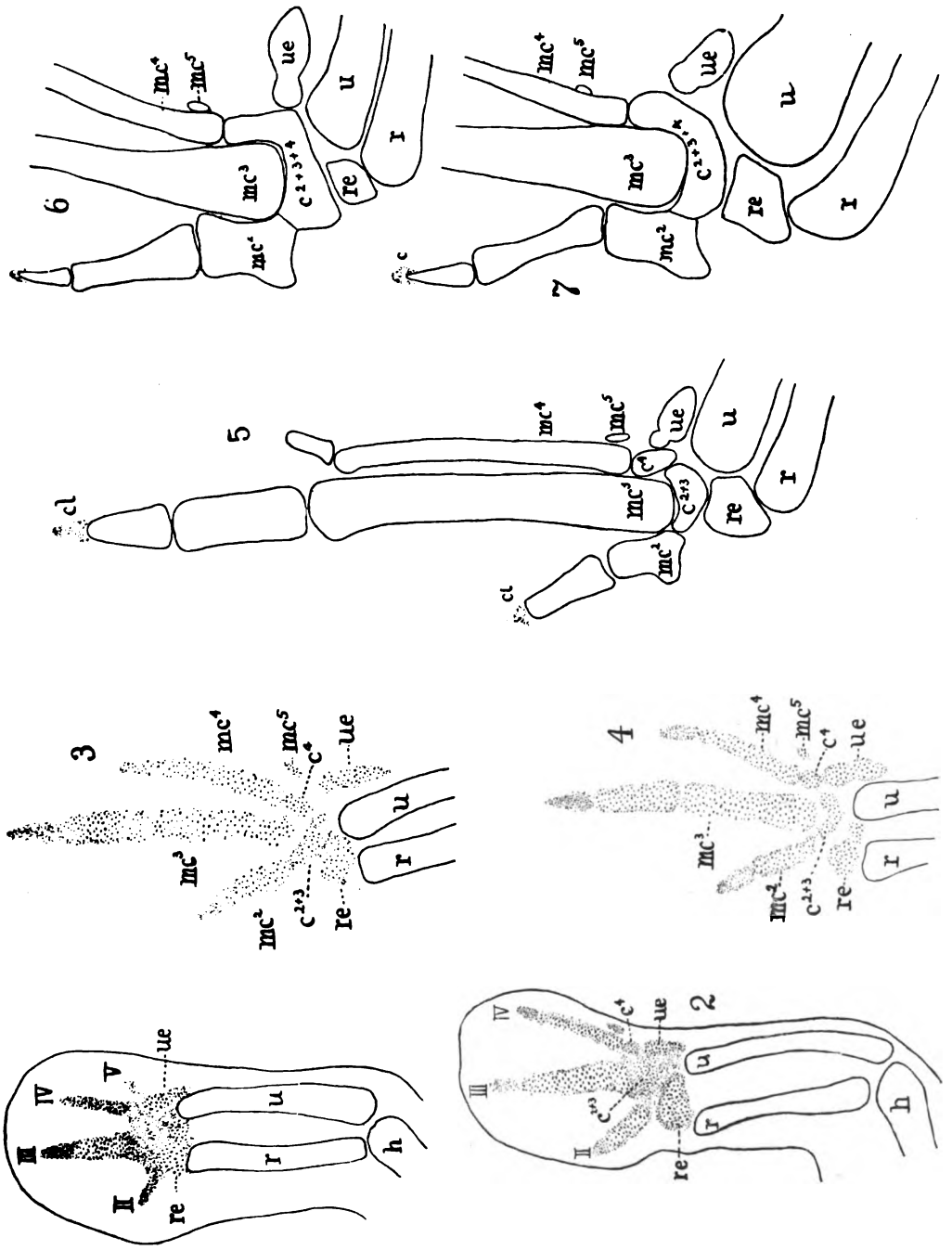

Leighton—Wing of Sterna.

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TUFTS COLLEGE STUDIES, No. IV.

THE MORPHOLOGY AND CLASSIFICATION OF THE PAUROPODA, WITH NOTES ON THE MORPHOLOGY OF THE DIPLOPODA.

FREDERICK C. KENYON.

PUBLISHED BY THE CHARLES HYDE OLMSTEAD FUND.

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THE MORPHOLOGY AND CLASSIFICATION OF THE PAUROPODA, WITH NOTES ON THE MORPHOLOGY OF THE DIPLOPODA.

By Frederick Courtland Kenyon.

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HISTORICAL.

In 1866 Lubbock discovered the minute arthropod with nine pairs of legs, to which he gave the name of *Pauropus*, and which he regarded as the type of a new family, Pauropodidæ, and possibly of a new order—Pauropoda—of the Centipedes. In his excellent paper, "On Pauropus, a new type of Centipede," he thoroughly describes the external anatomy of two species, *P. huxleyi* and *P. pedunculatus*, as well as the hexapodial young of the former species. From the data thus obtained he concluded that "this little genus does not possess the characteristics of either order of Myriapods, but forms a link not only connecting the Chilopods and Diplopods together, but also bridging over to a certain extent the great chasm which separates them from other Articulata." The activity of the creature, the compactness of the body, the dorsal plates, and the elongation of the posterior legs seemed to give it some resemblance to *Lithobius*, but these characters appeared to be outweighed by the structure of the antennæ, the absence

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of jaw-feet and the anterior position of the generative organs. Against its union with the Diplopoda there stood the only apparent and not real formation of double segments, the unequal size of the legs, the claws of the feet, the fact that, assuming the apparent double condition of the segments, only the first pair of legs could be said to represent a single segment, whereas in the Diplopoda the three anterior pairs of legs are each borne by a single segment, and the character of the mouth parts, which he thought like those of Chilopods except in being rudimentary. As will be seen in the sequel, these difficulties are only superficial, and are much outweighed by the single fact of the similarity in position of the genital apertures. Later writers were more fortunate in their conclusions, but it is to be noted that to them the genus *Eurypauropus* was known.

The discovery by Packard, in 1871, at Salem, Mass., of a very small *Pauropus*, to be placed, apparently, between the *P. huxleyi* and *P. pedunculatus* of Lubbock, and Ryder's finding of *P. huxleyi* at Fairmount Park, Philadelphia, was of great interest, as extending the geographical range of the group and thus indicating ancient origin. There was then some reason for Packard's assumption of its great age when criticising ('70) Haeckel's speculations on the origin of articulates. "And when the type," he says, "became terrestrial we (still speculating) would imagine a form somewhat like the young Pauropus, discovered by Sir John Lubbock in England, which combines in a remarkable degree the characters of the Myriapods and the degraded wingless insects, such as Smynthurus, Podura, etc."

But of as much or greater interest as the extension of the range of *Pauropus* to America was Ryder's discovery, in 1879, of the slow-moving, highly armored *Eurypauropus spinosus*, which, so far as the peculiarities of segmentation in *Pauropus* are concerned, at once put to rest all doubt as to the diplopod affinities of the Pauropoda. Here was distinct evidence of the formation of double segments, and, moreover, similarities with a less dubious Diplopod, *Polyxenus*. These similarities he found in the shape and the superficial ornamentation.

The two genera, *Pauropus* and *Eurypauropus*, are so different, forming, as he points out, a parallel to the families Iulidæ and

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Polydesmidæ, the one having a cylindrical, the other a very much broadened, depressed and heavily armored body, that Ryder was entirely justified in forming a new family Eurypauropodidæ.

In 1883 Latzel added two new forms to Ryder's *E. spinosus* in finding his *E. ornatus* and *E. cycliger*, thus showing the genus to have a probable geological age almost as great as that of *Pauropus*. The description, in his valuable "Myriapoden der österreichisch-ungarischen Monarchie," of *Brachypauropus hamiger* is of value as offering a possible clue to the origin the double segments of other Pauropoda and of the generally recognized diplopods. This form would seem, from its structural characteristics, to form a link, as Latzel considers it, between the two older genera, and, if it could be shown to be broadly distributed, might in truth be considered the older form, but as it was found in only one place, "Känten, in Mittelgebirge zwischen Klagenfurt und dem Wörthersee," it may be either a late local form or the nearly extinct representative of an older, possibly cosmopolitan one. This, with *Eurypauropus*, forms his second family, Pauropoda tardigrada, while *Pauropus* forms the first, Pauropoda agilia. The group he considered to have some relationship with *Polyxenus*; for to Lubbock's remark on *Pauropus*, "In its general appearance, in its minute size, in the character of its antennæ, in the possession of clubbed hairs and long setæ, *Pauropus* . . . . does something to relieve the disagreeable monotony of the class" (Myriapoda), he adds, "Am meisten scheinen sie mit den Polyxeniden verwandt zu sein." Possibly, like Ryder, he saw a similarity in the ornamentation. The same conclusion was later maintained by Schmidt.

Since Latzel wrote, nothing has been added to our knowledge of the Pauropoda—although their relationship with the diplopods has been questioned by Kingsley, who, in his papers on the classification of Arthropoda, was led from the branched, seemingly crustacean-like antennæ and the apparent hexapodial condition of *one* segment, as shown in Ryder's figure of the young *Eurypauropus*, to describe them as of *incerti sedis*—until Schmidt published a preliminary paper in the Zoologischer Anzeiger in 1894 on the anatomy of *Pauropus huxleyi* Lub. This contribu-

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tion, brief and incomplete as it is, filled a long felt want, and added, with its description of strange peculiarities of structure, no little interest to that with which I had previously undertaken work on the same subject. The results given in the paper will be mentioned along with my own.

In the fall of 1893 *P. huxleyi* was found in the neighborhood of Tufts College, Mass., but not in sufficient numbers to allow of much progress in my studies. A year later, owing to the kindness of the late Dr. Ryder and Dr. J. S. Kingsley, some twenty specimens of *Eurypauropus spinosus* from Fairmount Park, Philadelphia, were placed at my disposal. At this time also I found *Pauropus huxleyi* again and in sufficient numbers to offer an abundance of material for a comparison of the two forms.

METHODS.

From the first I found considerable difficulty in killing the animals. Like the minute Thysanura they would remain on top of all aqueous solutions without so much as becoming wet, so that it was always necessary first to plunge them into absolute alcohol. Some were then immediately placed in Kleinenberg's picro-sulphuric acid, while others were left in the alcohol to harden. Finally, Carnoy's mixture of absolute alcohol, acetic acid and chloroform was tried and adopted as the best medium for fixing the animals. To fix them in an extended condition a camel's hair brush was dipped in the fixing fluid and then placed upon the animal upon the table. This left them perfectly straight, without in any way injuring them. When fixed sufficiently each was cut in two to allow an easy penetration of stains and other fluids. To obtain good sections it was found necessary, especially with the heavily armored *Eurypauropus*, first to saturate the animals with celloidin before imbedding in paraffine.

THE ANATOMY OF PAUROPODA.

EXTERNAL ANATOMY.

As intimated in the foregoing there is a broad difference between the three pauropod genera. In some respects *Pauropus*

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and *Eurypauropus* offer a parallel to the Chilopoda and Chilognatha, the former being agile in its movements, and clothed with a thin dermal covering, while the latter is slow-moving, flattened, covered with a thick chitinous spiny armor and letusimulates upon the slightest provocation, rolling itself into a ball like a sow-bug. In no case have I seen such actions in *Pauropus*, but according to Ryder ('78), "the little fellows when roughly handled rolled themselves up and 'played possum' as do some Diplopods." The third genus, *Brachypauropus*, differs from the other two in the segmentation. In *Pauropus* and *Eurypauropus* there are six distinctly marked dorsal plates, each of the four succeeding the first covering two pairs of legs. In the later genus the diplopod condition is indubitable, and led Ryder to describe the animal as having only six body segments. On the other hand in the former genus, the third, fifth, seventh and ninth pairs of legs (diag. I and fig. 13) appear to come between the dorsal plates, thus much less clearly bearing evidence of a diplopodial segmentation. In *Brachypauropus* there is a dorsal plate corresponding to each of these foot-pairs. In movement it is so slow that Latzel includes it with *Eurypauropus* in his family Pauropoda tardigrada. In other respects it seems, from its description, to be like either of the other genera. Like Pauropus its chitinous cuticle is thin and spineless; like *Eurypauropus* it may sometimes be depressed in form.

It would seem from a consideration of this third genus, that there is in the other two no real exception to Savigny's law, and

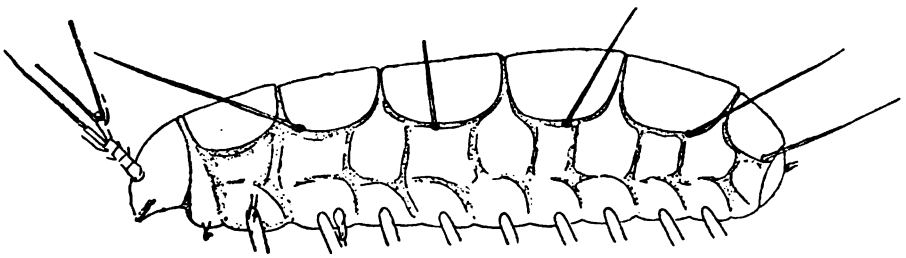

DIAGRAM I. EXTERNAL SEGMENTATION OF PAUROPUS.

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that, counting a segment shown distinctly in *Pauropus* and *Brachypauropus* between the head and the first pedigerous segment, together with an anal and a preanal legless segment, there are at least twelve body segments as illustrated in the diagram (diag. I). The dorsal portion of the first segment is very much reduced in *Pauropus* and is unsupplied with a "plate" like the others. In *Eurypauropus* it together with the head is completely covered by the greatly developed first dorsal plate (Fig. 64) which Ryder took to represent the first body segment. But in both forms it is distinctly marked ventrally by two large sac-like swellings, each of which bears a single protuberance representing, probably, the persisting coxæ of a pair of appendages. This seems the more probable since each protuberance bears a branched hair very similar to those occurring on the coxæ of the anal legs (fig. 16). This number of segments is further demonstrated by the so-called pleural folds, a pair of which, corresponding to the third, fifth, seventh and ninth leg-pairs in *Pauropus*, crowd up into the space between the dorsal plates behind the first. (diag. I.)

In the triangular head, so far as one may be able to judge from the number of appendages, there are three segments, corresponding to the antennæ, the mandibles, and the maxillæ. In this respect the Pauropoda are in harmony with the Chilognatha, where, as appears from embryological evidence, there are but two pair of appendages represented in the mouth parts. But, as we shall see later, there is other evidence of cephalic segmentation and possibly there are more segments in the chilognath head and in that of Pauropoda than the number of appendages would indicate.

The mandibles, shown in figures 6, 9 and 10, are joined to the head as in some of the Thysanura and have a large wing-like hinder portion that extends far back into the head (fig. 2). At the outer ends they are furnished with several sharp conical teeth. The maxillæ, but little developed, form a part of the lower lip, which Latzel, doubtless correctly, compares directly with the gnathochilarium of the better known Diplopoda. Between these two pairs of mouth parts lies a hypopharnygeal framework of chitin further recalling chilognath characteris-

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tics. This will be best understood from the figure (fig. 9), taken from Latzel, of the mouth parts of *Eurypauropus ornatus* and that of *E. spinosus* (fig. 6).

THE ANTENNÆ.

Much more worthy of note are the peculiar, branched antennæ which, to Lubbock, Latzel, Ryder and Kingsley, recalled the branched appendages characteristic of the Crustacea. These arise very close together (fig. 2) from the anterior surface of the head and are composed of four short, subequal joints, forming a basal, and two articulate branches forming a distal portion (figs. 1, 2, 5, 11, 18 and 23). The twin joints arising from the fourth differ considerably in their relation and size in the different species. In *Pauropus huxleyi* (fig. 23) the outer one—*stylus angustior* of Latzel—is considerably longer than the other (*stylus latior*). Upon its end is borne a single long flagellum-like hair. From the *stylus latior* two such hairs arise, and between them, borne upon a pedicel in *Eurypauropus* and in *Pauropus pedunculatus* and *lubbockii*, but sessile in *P. huxleyi* is a peculiar structure of possible sensory function, which Latzel terms the *globulus*.

The structure of the flagella was described by Lubbock as reminding one "very much of the toy snakes, which consist of a number of saucer-like appendages united by their middles" and Ryder ('79), in his description of *Eurypauropus*, gives a similar comparison, for he says, "These filaments, in minute structure, are very similar to those of the old genus, being composed of saucer-like disks, which are superimposed in a linear series and united at their centres to each other by delicate but very short pedicels." In his earlier paper ('78) on *Pauropus huxleyi* he says that "with a magnifying power of a thousand diameters ..... I have been unable to decide whether they are mere annular processes encircling the central axis of the style, or whether they are separate segments, though the flexibility of the styles would indicate that they were segmented." Latzel describes the structure as "feingegliederte Geiseln." Schmidt ('94) on the other hand considers them "nur fein geringelt"

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and describes them as each provided with a fine nerve running to the end. Still as to this point he is in doubt, for in a foot note he adds "Möglich ist es das es auch nur ein Canal ist; bei der Kleinheit des Objects kann man es auch mit den stärksten Vergrösserungen nicht unterscheiden."

My own observations accord with those of Schmidt that the flagella are in no proper sense articulate, but simply ringed. Without doubt they are directly comparable to the clavate hairs found on the antennæ, joints, and head of all forms, and on the dorsal plates of *Pauropus*. The rings are formed by a series of equi-distant constrictions or swellings, beginning, except in *P. pedunculatus*, a little distance from the base, thus leaving an unringed proximal portion, and ending with a large ovoid annulus. About the middle of each annulus there is a circle of very fine short hairs or spines that appear against the surface of the ring as fine short striæ. In optical sections of the ring they are seen to project, and possibly may be compared to the dentate projections on the hairs of *Polyxenus*.

Considerable variation is seen in the flagella in the different species. In all, that arising from the *stylus angustior* is much the longest. In *Pauropus huxleyi* and in *Eurypauropus spinosus* and *ornatus* the other two are nearly equal, the inner one being only slightly shorter. But in *Pauropus pedunculatus* (fig. 18) the inner one is considerably shorter and arises, apparently, from the side of the stylus.

That the earlier observers should have mistaken the structure of these extremely developed hairs—for that is all, in fact, that they appear to be—is not surprising, when one considers that probably only specimens *in toto* were studied. With magnification no higher than one thousand diameters, especially in the case of the small *Pauropus*, upon hasty observation, the constrictions look deeper than they really are, but magnified some fifteen hundred or two thousand times they appear as represented in figures 22, and 24—27. In some cases bubbles, apparently of air, are to be seen in the annuli in specimens mounted in glycerine jelly (fig. 26-27). Seen in section under a magnification of only nine hundred times the shallowness of the constrictions (fig. 26-27) in the hairs of *Eurypauropus* is very distinct.

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Further a protoplasmic thread is plainly visible, shrunken from the chitinous walls of the hair. That there should also be present a nerve filament, as Schmidt supposes, is, of course, possible, but it is not to be distinguished, by the methods of staining employed, from the protoplasm giving rise to the chitinous walls. In no way does a flagellum appear essentially different from the ringed hairs to be found on the joints of the antennæ and on the body (fig. 23, 35 and 38), except in degree of development.

In the distal ends of the *styli* (fig. 36-37) there appears to be a small ganglion, distinguished by its shape and its more elongate nuclei from the surrounding hypodermal cells. Usually the outlines of this are so hidden by hypodermal nuclei that it is recognized only with difficulty. In one case (fig. 36) in a *stylus angustior* of *Eurypauropus* the structure was plainly seen.

The *globulus* of the *stylus latior* is of great interest from its peculiar structure. In *Pauropus huxleyi* it appears as a small globular body upon a short style (fig. 22-23). In the other species and in *Eurypauropus* it is at the end of a long stalk (fig. 18 and 25). In all cases the globe is made up of an outer circle or calyx of ten or twelve fine hairs, closely hugging an inner globular portion—the expanded end of the stalk as shown in figures 22 and 34. In macerated specimens the communication between the bulb and the stalk is free, and in specimens otherwise prepared no membrane or partition is to be seen shutting off the space, but in specimens freshly mounted in glycerine jelly, the bulb has a bluish hue different from other parts of the organ as though it were filled with a liquid. This hue changes in specimens passed through the different preserving fluids and paraffin to one identical with that of the stalk, or so nearly so that the difference can be accounted for by the difference in the thickness of the chitinous walls. In no case did the contents of the bulb or of the stalk take a stain. But as the organ is missing from sections where the protoplasmic contents of the flagella were stained, this amounts to little.

Working upon *Pauropus huxleyi*, where the organ is somewhat less favorable in size than in *Eurypauropus*, Schmidt ('94)

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appears to have fallen into error, if my observations are correct. He figures the organ diagrammatically, and describes it as consisting of a "kugeligen, durchsichtigen Chitinkapsel, die eine zweite Knopfartige, auf einem Füsschen sitzende Kapsel einschliesst. In der Mitte der inneren Kapsel dringt ein nerv ein, der mit einer Erweiterung endigt. Die aüsser Kapsel ist mit einer sich durch Hæmatoxylin färbenden Flüssigkeit gefüllt und aussen von zehn bis zwölf die Kapsel umfassender anliegenden Borsten umgeben." According to my observations, and to those to whom the organ was shown, the nerve described as ending in an expansion is nothing more than the inner cavity of the bulb, and the first or transparent capsule filled with a fluid staining with hæmatoxylin is merely the space between the bulb and its calyx of hairs. The fact that in some of my specimens a bubble of air has been caught in this space, readily explains how a bubble of hæmatoxylin similarly retained might give rise to the appearance of a stainable fluid in a thin walled capsule. The inner or second capsule of Schmidt is my bulb.

So peculiar an organ must have some sensory function, possibly auditory. The calyx of hairs is so situated as to readily be made to vibrate against the liquid-containing bulb, from which the motion might be communicated to nerve endings from nerve cells in the tip of the *stylus latior*. The absence of nuclei in the stalk would seem to prove the whole structure a modified hair.

The conclusion arrived at with regard to the flagella may, it seems to me, be formed concerning the *stylus angustior* and its flagellum taken as a whole. This supposition seems to be supported by the peculiar branched hairs found on the coxæ of *Eurypauropus* (fig. 40) and by the form of certain ventral hairs of *Polyxenus* (fig. 41) as well as by what appears among certain coleopterous larvæ as shown at *a* in figures 28—33, or by the caudal styliform hairs (fig. 42) of *Pauropus huxleyi*, or, if Haase's conclusions be correct, by the ventral or abdominal appendages of *Scolopendrella* and certain of the Thysanures. Certainly there appear to be no muscles running into the styli. At all events the occurrence of accessory terminal hairs, spines,

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or joints—whichever from their degree of development one chooses to call them—on the antennæ and palpi of tenebrionoid beetles at once excludes the possibility of any one claiming for Pauropoda a near or remote direct relationship with Crustacea merely on the grounds of the biramous or triramous appearance of their antennæ. Much more plausible is the comparison made by Packard ('83) with the two-jointed terminal sensory spines of the chilognath antennæ (fig. 21). In life, the animal, as it moves about, uses its antennæ very much like a *Julus*, continuously and rapidly striking the surfaces before it with the tips of its outspread flagella.

THE SO-CALLED EYE.

On either side of the head is a large eye-like spot (fig. 2) which Lubbock presumed to be an eye, and which Latzel mentions as a possibly photoscopic eye. The spots are as well marked in *Eurypauropus* as in *Pauropus*, but Ryder does not seem to have discovered them, for he says "Eyes seem to be wanting, indeed the manner in which the first segment overhangs the head, would lead one to suppose that vision would be obstructed, rendering eyes useless." Schmidt could not distinguish the structure in *Pauropus* either in specimens mounted in toto or in sections. In my preparations they are perfectly plain, but they show no evidence of an eye-like structure, being lined with hypodermal cells not different in appearance from such cells elsewhere. The cuticle is only simply a little thinner than on the rest of the head. Nor is there to be distinguished in the brain either an optic ganglion or an optic nerve, as one might expect, if the structure represents the remains of an eye in an ancestor. Hence it seems possible to explain them only as simple dermal markings.

THE LEGS.

The nine pairs of legs in *Pauropus* are relatively long, increasing in length posteriorly, and remind one of the legs of *Lithobius*. In *Eurypauropus* they are relatively somewhat shorter and stouter, never showing in life much more than their extreme tips from beneath the depressed, broadened body. All

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but the first and last pair are made up of six joints in both genera (fig. 17—16). After the coxa the next three joints are subequal in length; these are followed by a short joint and this by the long, slightly curved sixth joint. In the first and anal legs the fifth or short joint is lacking (figs. 4, 15 and 16). Besides this they also differ from the rest in being smaller and shorter.

Terminating each leg is a strong claw (fig. 17) at the base of which is a small ovo-reniform sucking disc. From under either end of this projects, at right angles to the central claw, another small claw, making three claws in all, forming the foot. Under high magnification the marginal raised rim and central depression of the disc are readily distinguished. Near the end of the sixth leg joint is a small stiff curved hair and near its proximal end in the anal legs another very long one, indicating, possibly, that the proximal end is equivalent to the fifth or short joint in the other legs. Upon the other distal joints is a similar hair, and on the ventral side of the coxæ and the second joint, in *Pauropus huxleyi*, a highly developed, ringed curved spatulate hair. On the anal legs these hairs are further modified by having a spatulate branch, seemingly articulate. A similar branched hair is found on each of the papilliform processes arising from the ventral swellings of the first body segment, which, as already mentioned, are doubtless the remains of articulated appendages.

In *Eurypauropus* these ventral hairs (fig. 40) consist of an enlarged basal portion, from the tip of which arises a long slender, annulated hair. In those of the anal legs there is a branch, or short, smooth, slightly curved accessory hair arising beside the base of the other.

THE CUTICULA, ORNAMENTATION.

The cuticle of *Pauropus* everywhere presents a smooth surface and nowhere differs very much in thickness as compared with the differences found in *Eurypauropus*. Ventrally and laterally it is thrown into folds by internal muscular attachments. Above each leg there is a large fold, and above this another—the so-called pleura—extending to the dorsal plates, between

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which those corresponding to the odd leg-pairs are crowded (diag. I and fig. 13). The dorsal plates are decidedly arched and rounded, otherwise they recall somewhat the similar plates of the chilopods. Across each are two rows of clavate, ringed hairs, which also occur scattered over the head and at the end of each antennal joint. Besides these clavate structures there are, on the head and antennæ, long, curved, tapering hairs (fig. 23, 35). One of these arises from the side of the *stylus latior*, a fact that makes this structure appear more like a real joint than its companion stylus, thus making five joints in the antennæ as has been generally described. Posteriorly the clavate hairs become less and less clavate until in the anal segment they are very slightly tapering. The ringing seems in the large hairs to be due to the same characters that appear in the antennal flagella.

In some of the tapering hairs the same ringing appears, but towards the tip, especially in the hairs of the anal segments and the lateral, tactile hairs, distinct hair-like projections may be seen under high magnification. Some of these hairs therefore present a slightly feathery appearance towards the end.

From just beneath the lateral edges of each dorsal plate except the first, there arises a very long, tactile hair, with a bulbous base, connected internally with an oval mass of ganglionic cells (fig. 43) which send several nerves to the ventral cord. The first and second hairs arise from near the anterior corners of their corresponding dorsal plates and point forwards, while the fourth and fifth arise near the posterior corners and point backwards. The third is directed laterally and arises near the middle of the plate margin.

In *Eurypauropus* the dorsal portion of the body is very much modified, the six dorsal plates being formed by a thick chitinous cuticle (figs. 45-47), which, in sections, splits into an inner, thick, light-colored layer, and an outer, thinner, dark layer. Over its surface, thickly and more or less regularly arranged, are numerous peculiar hooked spines, which to Ryder recalled in some degree the dentate hairs of *Polyxenus*. Between them are many small wart-like protuberances (fig. 48) each rising from the centre of a small ring of similar but very minute papillæ. A

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row of similar papillæ connects each of the protuberances with its neighboring protuberances and with the bases of the hooked spines, thus producing a hexagonal reticulate appearance (fig. 48). The spines consist of a pillar-like basal portion (figs. 45, 46) into which projects a large protoplasmic process from a single hypodermal cell. Distally this is somewhat expanded. Over the top of the pillar fits horizontally a cap-like spine with its apex directed backwards. This is of a somewhat darker color than the rest of the structure and appears in transverse sections to be articulated by means of a ball-and-socket joint to the process fitting into the pillar. They are more or less easily movable, though not properly speaking jointed. Possibly they are deciduous, which would make Ryder's comparison more striking. They do not, however, brush off readily, as in the case of the hair tufts of *Polyxenus*. Probably they are modified hairs raised on the pillar and to be compared with the flattened scales of the Thysanura and Lepidoptera. In *Eurypauropus ornatus*, the lateral ones are broad, leaf-like, and ornamented with a raised linear net-work.

Besides this peculiarity, in *E. ornatus* the dorsal hook-spines are arranged on the plates in definite raised areas around depressed areas covered only with wart-like protuberances. According to Latzel ('84), "Die ganze, stark gewölbte Oberfläche ist mit wärzchenförmigen Körnchen dicht besetzt, welche in durchfallendem Lichte ebenso vielen Perlchen gleichen. Mit aus nahme der zwei letzten zeigt jeder Rückenschilde vier er hab ene Längsrippen oder Felder eingetheilt wird, auf dem halb kreisförmigen ersten Rückenschilde sind die beiden mittleren Längsleisten durch eine Querleiste verbunden, so dass das Mittelfeld in zwei kleinere Felder getheilt wird. Auf dieselbe Weise ist das an das Mittelfeld zunächst angrenzenden Feld rechts und links in zwei Felder getheilt, so dass man am ersten Rückenschilde acht tiefer liegende Felder unterscheidet, während am sechsten Rückenschilde nur eine (mittlere) Längsleiste auftritt, wodurch seine Fläche in zwei Felder getheilt erscheint. An dem sehr kleinen Endsegments ist von einer Längsleiste nichts zu bemerken. Die Mittellinie der genannten Längsleisten wird durch drei oder vier oder meistens von fünf in einer Längsreihe

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hinter einander stehenden erhabenen Körnern eingenommen, welche auch auf den Querleisten des vordersten Schildes stehen."

In the lateral margins of the fourth to the sixth plates of *Eurypauropus* there is hollowed out a small notch, upwards through which project the five pairs of long tactile hairs. By their aid Ryder ('79) endeavored to make out a segmentation of the animal corresponding to the number of pairs of legs. "I am led," he says, "to surmise that the notches at the sides of the third, fourth, and fifth segments of the adult possibly indicate that these were primitively compound, and in reality represent two segments fused together, which would make nine in all, counting the others as single." But he adds that there is quite as much reason for believing the others compound. To me they seem to have no particular segmental significance, but appear to have been formed merely because the tactile hairs would otherwise be prevented from projecting upwards in a position to be of the greatest use to the animal. The hairs, however, as shown in both genera by their position and innervation, seem to belong to alternate segments beginning with the third.

If *Pauropus* be considered, the position of the hairs and the manner in which the alternate pleuræ crowd up between the plates, indicate that in the latter we have to do with the hypertrophy of the tergal portion of one segment and the atrophy of the corresponding portion of another, rather than with the fusion of two dorsal plates. Should at some future date embryonic evidence be found for such a supposition there would then occur in Pauropoda a condition of growth nearly parallel to what occurs in the Decapod Crustacea, where the carapax is formed by the hypertrophy of the tergal part of a few anterior segments.

The lateral tactile hairs in *Eurypauropus* are similar in appearance, except the fourth pair in *E. spinosus* and all in *E. cycliger*, to those of *Pauropus*. The fourth pair in the former species differ in being shorter, and in terminating with a smaller or clavate tip (fig. 44). In the latter species Latzel ('84) describes all these hairs as being finely feathery, and the fourth pair as being clavate and very much shortened. The feather-

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ing is doubtless different from that in these structures in *Pauropus* and *E. spinosus* only in degree.

A CARTILAGE-LIKE FORMATION OF THE CUTICULA.

A peculiar modification of the cuticula appears at the posterior end of the dorsal plates where it is bent back under the plate to connect with the anterior end of the one next following. Here the two layers thus produced are united with one another by small cuticular pillars, so that in sections small cavities filled with one or more hypodermal cells are to be seen, and recall the appearance of the cartilage which Patten claims to have found in *Limulus*. There is the difference, however, that in the animal under consideration the cuticula is very thin compared with that of the margin of the carapax of *Limulus*, which of course accounts for there being but a single layer of the cavities as shown in the figures (figs. 45, 46). The explanation is obvious; the turning back of the integument by one plate overlapping another forms two layers of hypodermal cells which may be crowded out of position, and as a consequence form the pillars. Were the animal to be increased to the size of *Limulus*, the then enormously thicked secretion would very naturally cut many of the hypodermal cells off from their fellows and give the appearance of lacunæ.

INTERNAL ANATOMY.

Between *Pauropus* and *Eurypauropus*, so far as I have been able to learn, the differences in the structure of internal organs, with one or two prominent possible exceptions that will appear later, are differences merely of size, *Pauropus* being somewhat the smaller animal. Hence a separate description is entirely unnecessary.

ALIMENTARY CANAL.

The intestine (fig. 85) is very simple in structure, consisting of a very short foregut (fig. 83, *f. g.*), communicating with the un-

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der side of the anterior end of a long, simple mid-gut, joined posteriorly to the small constricted anterior portion of the simple hind-gut. The walls of the fore-gut are extremely thin and delicate, showing no evidence of a muscular outer coat nor of a chitinous intima, though the latter is in all probability present. The nuclei of the cells are very small and elongated mainly antero-posteriorly. The structure rises perpendicularly from the mouth to a position between the circumoral commissures where there is a slight enlargement. From this it passes backwards at right angles and for an equal distance, to the mid-gut, with which it unites without the least indication of a valve such as is generally found in insects and diplopods. Just behind the anterior half and apparently in front of the first ganglion there are two muscle bands (fig. 83) apparently connecting with it at the angle mentioned. The whole tube is so short that the mid-gut very nearly abuts against the hinder surface of the brain.

The epithelium of the gut is very peculiar from the enormous size of its cells, their nuclei and contents. The cells vary somewhat in shape, from nearly cubical to thick and flat, (figs. 50, 54, 69, 70,) according to the degree of distension of the walls, and form internally a nearly uniform surface. Nearly all of them, from end to end of the gut, are thickly crowded with small crystals (fig. 51) of some, probably, carbonate salt. These, when perfect, have a rhomboid shape and reach a size as great as 4.5μ, taking the longest diagonal. The greater number are, however, not more than one fourth of this size, and very few present perfect angles. Many appear broken and rounded. Viewed by reflected light they are whitish, and by transmitted light, black. According to Schmidt ('94) they are doubly refractive. They are found in sections of all specimens both of *Pauropus* and *Eurypauropus*, except in those passed through acid, and may be distinguished in both young and old animals, dipped in alcohol and quickly mounted in glycerine jelly, by the black, granular appearance that they give the intestine. Hence it is not likely that they are caused by the action of reagents upon some peculiar constituents of the cells. Further, small groups of them are often found in the lumen of the gut.

Whether they are formed by the cells or are injested, is some-

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what difficult to determine. In one case a small bunch of them was found in the posterior lumen of the fore-gut, which would seem to indicate that they are injested, but generally the lumen of the whole intestine is too free from them to support such an idea. Further one would expect in such a case crystals formed of different substances, as of quartz and feldspar, but no crystals are left upon treating sections with weak hydrochloric acid. That they cannot be crystals of uric acid, as Schmidt supposes to be possible, is proven by the fact that they are soluble in hydrochloric acid. Probably, since one would scarcely suppose that such an animal would select carbonate crystals exclusively or have any physiological use for them in so large numbers, they are to be regarded as excretions of calcium carbonate, or at least of a carbonate, that has been either separated from the humus eaten, or formed from it. Nowhere in the animal kingdom, so far as I have been able to learn, has an exactly parallel condition been shown to exist. In certain of the annelids, however, there is a certain modified portion of the mid-gut performing the function of excreting calcium carbonate, which may offer a partial parallel, or perhaps even have a phylogenetic significance. Certainly the formation of such crystals in the intestine can have nothing to do with the absence of Malpighian tubules, for in *Eurypauropus* both crystals in very large numbers and Malpighian tubules occur.

These epithelial cells are further remarkable from the great elliptical nucleus with enormous nucleolus that each contains. Otherwise their characters are little different from digestive cells elsewhere. Sometimes the few cells containing no crystals, and after treatment with acid, the others show merely a granular cytoplasm, while at others the cytoplasm is arranged in a mesh-work of granules (fig. 51 to 69). The great nuclei may measure fully 12 to 15μ in length, while the mass of chromatin forming the nucleolus may be as much as 3$\frac{1}{2}\mu$ in diameter. Generally very little chromatin appears outside of the nucleolus and then only as fine scattered granules; hence the nucleus is much more transparent than the surrounding cytoplasm, from which the nucleus is marked off by a thick nuclear membrane.

Surrounding the epithelial layer is a membrana propria, which

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in some cases, in *Eurypauropus*, appears thicker than in others. This does not seem to be all due to the degree of extension of the tube, for here and there around the rim often appear very small stained masses of a nuclear aspect, indicating the presence of a thin outer layer of cells—the very poorly developed muscularis. In the smaller animal, *Pauropus huxleyi*, neither Schmidt nor myself have been able to distinguish such a layer in this portion of the intestine. Near the beginning of the hind-gut the layer becomes very much thicker, though not quite so thick as shown in figure 59, the thickness here being largely due to the angle of observation.

At the beginning of the constriction, or at the junction of the mid and hind-gut, the crystals disappear from the epithelial cells, and these change in their shape and in the size and general position of their nuclei. Figure 54 shows a longitudinal section, magnified some seven hundred and ninety times, in which the cells of the mid-gut appear at the left. These it will be seen, become smaller and smaller towards the end, while the cells of the hind-gut become suddenly columnar and have smaller nuclei. The latter occur as near the base of the cells as in the case of the large nuclei of the mid-gut, and are arranged with their longer axis radial with respect to the tube. These cells vary considerably in shape, from columnar to cuboidal or even flat (fig. 53), both in the same and in different individuals. In some cases they project into the lumen of the tube, in this respect differing from the cells of the mid-gut, which generally present a nearly uniform inner surface. About this section of the intestine, as in the last, there is formed a distinct membrana propria, and a more evident outer layer of cells.

After bending back over the mid-gut, the constricted intestine joins the side of the anterior end of the large conical rectum (fig. 55, 56). Here the epithelial cells become lower until finally they form a very thin layer clothed internally by a chitinous intima. This is distinguishable also in the posterior end of the small tube, but it gradually thins away anteriorly. The great size of the rectum is caused by the great thickness of its muscular coat, which consists of two layers of dimly straited muscle cells. The internal layer runs longitudinally; the other is

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circular. In the latter, one cell seems to complete the circumference. Towards the end the rectum becomes smaller until it opens through the end of the anal segment.

Two large glands occur, one on either side of the brain, which send their two ducts to the inner part of the mouth where they open separately and ventro-laterally. They, therefore seem to be salivary glands, comparable to the long, salivary glands of the Chilognatha. The cells of the glands are so closely packed that no lumen whatever is distinguishable, but the presence of small nuclei scattered about between the large glandular cells seem to indicate a more or less racemose system of collapsed tubes. The nuclei of the secreting cells are all large, but some are excessively so. In these the chromatin appears in the centre as a close snarl of one or more threads, with a large, clear space between it and the nuclear membrane (fig. 57). The walls of the ducts are composed of very thin cells.

Schmidt mentions another pair of glands of smaller size occurring in the head near the brain, but I have failed to find them in either *Pauropus* or *Eurypauropus*. In some of my sections there appears a small mass of cells not far from the side of the antennal lobes that might be mistaken for glandular masses, but these prove, after due study, to be the hypodermal cells of the large inner processes of the mandibles.

From the intestine, in the region of the junction of the mid and hind guts, there arise in the female *Eurypauropus spinosus* two tubes that run forwards along the sides of the intestine to the fifth or the fourth segment. Whether they occur in the male, I am unable to say, there being none in the lot sent me. The most noticeable feature of the tubes is their large size, increasing interiorly,—which seems mostly to be due to the large vacuoles that each cell in the anterior region possesses (fig. 58). But even where there are no vacuoles (figs. 60, 61, 63) they are proportionately very large as compared with the Malpighian tubes of insects and chilognaths. The lumen is very small and often seems entirely suppressed.

In *Pauropus huxleyi* no such tubes are to be found, which fact may have led Schmidt to suppose the crystals found in the cells of the mid-gut to be possibly uric acid. But in the neighbor-

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hood where Malpighian tubes should arise, there appear, among the cells of the fat-body, small groups of cells (fig. 62) that in section look very much like tubes, and may run through several consecutive sections. Whether, however, these may be the degenerate remnants of Malpighian tubes, or merely clusters of cells of the fat-body, which they also closely resemble, I am unable to say, since they do not appear to be connected with the intestine. They do not occur in *Eurypauropus* and they are slightly different in appearance and in arrangement from the fat-body cells elsewhere in the animal. It may also be said that they occur in both sexes.

To determine definitely whether the Malpighian tubes belong to the mid or hind gut, is of course impossible without following out the development of the intestinal tract. Their union with the intestine is very close to the junction of the mid and hind-gut as determined by the constriction of the tube and the change in the character of the epithelial cells, and they may be of ectodermal origin, but the sections shown in figs. 59 and 60 seem to indicate that they arise from the mid-gut. If this is really the case—as seemingly it must be, if no cells of ectodermal origin take part in the formation of crystals or otherwise bear so close a resemblance to the cells in the anterior end of the mid-gut—then the Malpighian tubes occurring here are not comparable morphologically with those of insects, or if their development has been correctly observed, with those of chilognaths.

THE NERVOUS SYSTEM.

The brain fills up the greater part of the head and even passes back into the first body segment. In *Eurypauropus* it even appears to lie, as seen in longitudinal sections (fig. 64), in the second segment. This is to be explained by the fact that the head is drawn back under the first dorsal plate, and as there is here no internal evidences of segmentation, the position of the brain appears abnormal. A little pressure properly applied shoves the head out in front of the plate. The posterior lobes do not then appear to overhang the fused first ventral ganglion.

Viewed from in front, or morphologically the top, the brain

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presents a triangular appearance, the apex of the triangle directed anteriorly. Between the large expanded posterior lobes forming the base of the triangle there is only a slight and shallow groove separating the two original lateral ganglia. Below these lobes, indicated externally by grooves and internally as seen in cross section (fig. 66) by nuclear grouping, are the two long antennal lobes. Anteriorly these approach one another and become fused with a large median unpaired frontal lobe (fig. 82). Just below this the antennal nerves arise close together and pass almost immediately into the antennæ.

Behind the frontal lobe and between the antennal lobes there is left a small narrow cleft (c. f. figs. 82, 83) that passes completely through the brain mass. Nowhere else, except in *Polyxenus*, have I found a similar condition. Through the anterior part of the compact brain-mass of this diplopod there is a small fissure through which several muscles pass to the pharynx. In Pauropoda these muscles do not occur. What the lobe thus rendered distinct from the rest of the brain is to be compared with, unless it be with the frontal ganglion of other Antennata, is not plain. If such a comparison be correct, then the ganglion has here become enormously enlarged, and the commissure between it and the rest of the system much shortened and thickened. Further the origins of these commissures have moved forwards into the brain mass.

The ganglionic nuclei are distributed over the brain surface in a nearly uniform layer, only ventrally, next to the intestine and in a small patch laterally (fig. 67) between the antennæ and postrior lobes, are they absent. No groupings are evident that would indicate other lobes than those described. If optic lobes have ever been present they now appear completely fused with the cerebral lobes proper, but this it may be remarked, is also the case with *Polyxenus* and many other forms where the optic nerves arise directly from the brain mass.

Schmidt evidently did not correctly make out the structure of the brain in *Pauropus huxleyi* for he says: "Das Nervensystem besteht aus zwei miteinander gänzlich verschmolzenen Kopfganglien und einem Bauschstrange. Die beiden Kopfganglien bilden ein eiförmige, compacte Gehirnmasse, durch welche der Vor-

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derdarm hindurchdringt. Vorn gehen von dem Gehirn nach unten hin gerichtet zwei dicke Antennennerven ab. Hinten geht der untere Theil des Gehirns (welcher dem unteren Schlundganglion entspricht) unmittelbar in den Bauschstrang über." In my studies I have found no difference between the brain of *Pauropus* and that of *Eurypauropus* except in size, and this difference is not so great as to obscure any of the structures so plainly shown in the latter genus. His failure to distinguish the different lobes is doubtless due to the plane of his sections and to his not employing any method of reconstruction. As may readily be seen from figure 64 the brain structure and its proper relations with the ventral cord would be very obscure in sections taken perpendicular to the ventral cord or to the section shown in figure 66, unless some method of reconstruction were employed.

This of course explains why he found the under surface of the brain passing directly into the first large ventral ganglion. In several cases my sections show, in both genera (figs. 64, 65) a long commissure forming one half of the circumœsophageal commissure, which becomes united with the brain through the lower, inner surface of the antennal lobe. If the subœsophageal ganglion were fused with the brain mass, one would then expect to find the mandibular and maxillary nerves arising from the brain. Such, however, is not the case. On the contrary, so far as I have been able with difficulty to distinguish them, they arise from the first ventral ganglionic mass as in *Scolopendrella* and other forms, where the subœsophageal ganglion has fused with the first ventral ganglion. I am by no means certain, however, that what I have taken for these nerves are such, since they are obscured by other details.

The ventral chain of ganglia shows nine distinct ganglia, decreasing in size posteriorly. Anteriorly they approach each other closely, until the first and second form, with the subœsophageal ganglion, a very large ganglion occupying the first and second segments of the body. The lateral halves of the cord are, as in Diplopoda, so thoroughly fused as to leave, at least anteriorly, no external traces of a separate condition. But in transverse sections there appear small median conical clusters of nuclei (figs.

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67-70) and sometimes a line of division, separating the halves. Posteriorly these nuclear heaps completely penetrate the cord so as to show small oval nuclear patches on the upper surface. The ganglionic cells are very numerous, covering the ventral, lateral, and the edge of the upper, surfaces of the cord. Posteriorly they thin out, leaving only one or two layers below and only small groups at the side. With the exception of the places of origin of the pedal nerves and in one or two instances of the space between a pair, the coat of cells is unbroken. Over the whole cord is a neural sheath, the nuclei of which form a dorso-median line. In some sections between the ganglia the sheath pushes down between the cordal strand to the nuclear heaps.

In the large anterior ganglion there is, in a reconstruction made upon millimeter paper, a faint indication of the component ganglia by lateral swellings. In a median longitudinal section (fig. 83) the nuclear grouping (shown by the shading lines) demonstrate at least one small posterior ganglion, from which, as shown by transverse sections, the first pair of pedal nerves arise, and a large anterior one. This is certainly large enough to be composed of two ganglia, and in view of the absence of a distinct subœsophageal ganglion, it is without doubt so composed. This tendency to cephalization in the ventral cord is further shown by the short space between the third and second ganglion as compared with the distance between the third and fourth. Between these two, however, the distance is slightly greater than between the ganglia behind the fourth. This is doubtless explained by the opening of the genital organs between them. In the union of the subœsophageal and the first ventral ganglia it may be said that *Pauropoda* corresponds with *Scolopendrella* and *Polyxenus*.

From the ventro-lateral side of each ganglion, a little behind the middle, the pedal nerves arise and pass down and outwards into the legs. Besides these no other nerves are to be seen arising from the cord in my preparations, except the nerves to the lateral, tactile hairs. These seem to arise from eight or ten processes of the cells on the side of the ganglion opposite the organ and are gathered into a small bundle, which follows a nearly straight course to the large oval sensory ganglion at the

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base of the hair (fig. 43, 44 a). This seems to be made up of a large number of cells and sends a small neural bundle into the base of the hair.

No evidence whatever could be found of the existence of a so-called sympathetic system.

BODY CAVITY AND FAT-BODY.

There is no distinct space left in the animal as a body cavity, but between the muscles and all the other organs there are to be found great cells comparable to the cellular masses in other forms, which for want of a better name have been called the fat-body. These cells appear proportionally much larger than elsewhere, reaching a size in *Pauropus* of 25 by 13 microns or more and in *Eurypauropus* of 46 by 30 microns. They appear very much vacuolated (fig. 50, 58). Sometimes a single cell may appear in section to have three or four great vacuoles with only small granular protoplasmic threads between them. Generally, however, the vacuoles are of moderate size. In the cytoplasm are to be found large spherical granules that take up the general or cytoplastic stains. Colored with picric acid the larger appear like globules of a thick, yellow oil, or not very unlike the yolk spheres in nearly mature eggs, except in their generally smaller size.

Besides their large size and consequently small number of them seen in a cross section of an animal, these cells of the fat-body are further remarkable for their enormous nuclei and nucleoli. In general, as is well-known, the nuclei of fat-body cells are considerably larger than the nuclei of other cells, but here they are exceptionally so. In *Pauropus* they may measure as much as 8 or 9 microns in diameter. Schmidt describes them as being as large as 10-11μ, but I find none quite so large. In *Eurypauropus* they are a little over 11μ in diameter. Usually they present a nearly circular or oval outline, but now and then one is found with a protuberance as though it were budding. All of them are thickly dotted with small chromatin granules so that they appear deeply stained; and in the midst of the granules each contains an enormous globular nucleous of a homoge-

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neous appearance. This is proportionally and actually somewhat larger than that found in the nuclei of the cells of the mid-gut, reaching a size in *Pauropus* of 3, and in *Eurypauropus* of 7 microns.

In the possession of such enormous nucleoli in these nuclei the Pauropoda seemingly stand alone among Arthropoda. In their supposed nearest relative, *Polyxenus*, no such nucleoli occur, the nuclei being simply coarsely granular like the body of the nucleus in the fat-body cells, in the pauropods. In sections of the diplopods, *Polydesmus*, *Julus*, *Lysiopetalum*, and *Brachydesmus*, in *Scolopendrella*, the chilopods, various Thysanura and higher insects I find in the fat-body and mid-gut no nucleoli as large, nor do I find either figures or descriptions of such. In the diplopods, however, the small cells of the mid-gut possess proportionately as large nuclei and nucleoli; the cells of the fat-body and their nuclei are nearly as large, but the nucleoli, when these are distinct, are of a diameter less than half as great as those in Pauropus.

THE HYPODERMIS.

The single layer of flattened cells forming the hypodermis is not of the same thickness throughout. In the dorsal region, where the cuticle is thicker, the cells are somewhat more numerous and consequently form a thicker layer than they do ventrally or laterally. Especially is this the case under the thick heavily armored plates of *Eurypauropus*. Here the cells appear filled with deeply staining protoplasmic granules and show little or no evidence of bounding walls between each other. In some cases, however, where sections have been slightly torn, the cell-boundaries may be seen to be present, though obscure. Ventrally and laterally the cells are to be distinguished mainly by their nuclei. These in section are elongated and contain numerous fragments of deeply colored chromatin. Whether there is a basement membrane cannot be readily determined. The cells of the fat-body apply themselves closely against the hypodermis and their cell walls give the appearance of a thick (compared with the hypodermis) structureless membrane. There is no

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evidence of a basement membrane separated from the hypodermis by the fat-body, such as is said by Fernald ('90) to occur in the Anurida. When the cells of the fat-body are torn away the membrane goes with them, leaving no connecting shreds, while no membrane is visible upon the freed surface of the hypodermis.

Under the large dorsal spines of *Eurypauropus* a hypodermal cell is often seen partly crowded upwards out of the layer, and from it a long protoplasmic process projects into the base or pillar of the spine in which it expands somewhat distally (figs. 45, 46). In sections it does not appear to penetrate the horizontal hook, but in looking at the hooks against the surface of the plate there seems to be a narrow median line in each, as though it were penetrated by a fine channel. Such is without doubt the case, since the chitinous hook must be secreted. When the cellular layer is torn away from the cuticle, many small, conical and thread-like projections may be distinctly seen, which have been pulled from the smaller cuticular protuberances.

THE MUSCULAR SYSTEM.

The muscular system is not very different from that found in diplopods generally. Between the two genera, *Pauropus* and *Eurypauropus*, there is a slight, though not essential difference in the direction of the muscle bands, due to the rounded body in the one and the depressed and laterally extended body in the other. The arrangement of the muscles in the latter genus recalls that in *Brachydesmus*. Three chief systems are to be distinguished:—a dorso-longitudinal, a ventro-longitudinal, a dorso-ventral, and a ventro-transverse system. Each is made up of a right and a left group.

In the dorso-longitudinal system in *Eurypauropus* the muscles run from plate to plate. Posteriorly they are attached to the anterior edge of one plate just where the thin dermal fold turns backwards to the hinder edge of the next anterior plate, and anteriorly to a small cuticular invagination that forms a shallow groove across the plate about a third of the length of the plate from the anterior edge, or just under cover of the hinder edge of the next anterior plate. In the dorsal muscles of the

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head the posterior attachment is not at the anterior edge of the plate, which seems to have developed forwards, but near its transverse median line. Anteriorly they are attached to the hinder edge of the head. From this it will be seen that, excepting the first plate, there is anteriorly, a small space under each which is free from muscles of this system.

The muscles of the ventro-longitudinal system are shorter than those just described, and form a continuous band of muscles a little below and to one side of the nerve cord. Each individual muscle spans a segment and is attached at either end to an intersegmental transverse infolding of the cuticle.

In the dorso-ventral system several groups are to be distinguished according to their insertions. They all arise from the middle third of the lateral half of a dorsal plate. One group of two or three muscles, the dorso-coxal, passes perpendicularly between the cells of the fat-body to the underlying coxa. Another, the dorso-sternal, arising from the outer portion of the dorsal area of muscular attachments, spans the space between the dorsal plate and the sterna, to a small median invagination of which it is attached. Arising inside the origin of the last are two groups of several muscles each, that pass obliquely to the pleural invaginations below, which they produce, and may be designated the exterior and interior dorso-plural muscles.

The muscles of the ventro-transverse system arise from the ventro-longitudinal system, or its attachments, and cross below the nerve cord to the coxa of the opposite side of the segment. Muscles from the plural folds seem to connect with their attachments in the longitudinal system.

In the head I have not been able to make out satisfactorily the distribution of the muscles, especially of the oral appendages. Some of the antennal muscles, however, seem to arise from a tendinous framework just below and within the angle formed by the mid-gut and pass to the antennæ of the corresponding side. From the same frame-work also arise two other pairs of muscles composed of two fibres each. The anterior pair become inserted at the same spot on the under surface of the mouth. Behind them another pair, but unlike the first, pass wholly outside of the circumœsophageal commissure, seemingly, into the lower lip.

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Histologically the muscles are not essentially different from those of insects, save that the transverse bands are somewhat dim. In most cases only dark and dim bands are to be seen, but where the muscles are extended, the so-called Krause's membrane and the adjacent light bands are distinguishable. In the muscles surrounding the rectum the banding is very obscure, yet appears to be really present.

From one to several fibres may constitute a muscle, and each seems to possess a sarcolemma. In some cases, as in the ventral muscles, the fibres seem to taper at one or at both ends into a short tendon. In other cases, as when attached to the cuticle, they appear to arise directly from their attachments. No where have I seen evidence of their being attached to the inner surface of the hypodermal cells, or to the basement membrane of these as described by Fernald ('90) as sometimes being the case in Anurida.

CIRCULATION AND RESPIRATION.

In none of the sections of either *Pauropus* or *Eurypauropus* can any evidence of a circulatory or tracheal system be found. Whatever circulation there is, must be between or through the cells of the fat body, which may also function in respiration, the necessary air being taken in through the whole body in *Pauropus*, or through the ventral surface in *Eurypauropus*. Possibly also, as Schmidt suggests, the enlarged lower surface of the first segment may function in respiration somewhat after the manner of the ventral sacs of Thysanura, as pointed out by Haase. Of this, however, I find no evidence from the presence of retracting muscles, and, it may be added that after watching the animals for some time under a magnification of some 115 diameters, I have seen no rhythmic contractions of any portion of the body that can be interpreted as breathing.

In this absence of a respiratory and a circulatory system the Pauropoda stand alone among the Diplopoda. It may possibly be accounted for by degeneration, or with equal probability by their never having been present, since such small animals would scarcely need them. A somewhat parallel condition is

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found among the smaller Thysanura, where the respiratory system is very poorly developed, even when present.

THE FEMALE GENITAL SYSTEM.

The female sexual organs are simple and of the primitive type generally described for the Diplopoda. The ovary consists of a large sac lying medially below the mid-gut, from the fourth or fifth segment backwards. It is crowded with ova, the larger of which are forced out laterally and forwards, leaving a central and posterior mass of very small ova. Among these the large granular nuclei of the ovarian epithelial cells are to be distinguished. These cells consequently possess very irregular outlines, and over the larger lateral ova are stretched into a thin protoplasmic layer (fig. 70). Anteriorly, however, they form a perfect cubical epithelium.

Leading from the anterior end of the ovary is a large *oviductus posterior*, with tall columnar glandular epithelium and narrow lumen. The large oval nuclei lie close to the bases of their cells, and these have a more or less reticulate appearance. Outside of them there is a thin layer of cells with small oval (in section) nuclei. There is no strong demarkation between the tall columnar cells of the duct and the low cubical cells of the anterior part of the ovary (fig. 67). The latter pass gradually into the former, which are tallest at the anterior end of the duct. Posteriorly this is somewhat flattened, but anteriorly it is rounded and pushed out from beneath the intestine to the right side of the body.

From the under side of the anterior end of this glandular portion of the oviduct a very much smaller *oviductus anterior* passes below the nerve cord, and, after making a long bend, opens to the exterior through a small round pore in the third segment, a little to the right of the mid-ventral line, and just a little behind the second pair of legs. The large cells, in the collapsed condition of the duct, appear approximately cubical and leave a very small lumen. Outside of them is to be distinguished the same thin layer of cells with small oval nuclei that surrounds the posterior portion of the oviduct.

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Near the external opening there is a slight expansion of the duct, forming a vagina (fig. 68). Into this opens the duct of the single *receptaculum seminis*, which forms a large spherical sac lying wholly below the nerve cord, and occupying most of the space between the genital aperture and the third pair of legs. In none of the animals sectioned did I find spermatozoa or other contents, nor was the vessel at all collapsed. Its thin walls consist of a layer of flattened epithelial cells with long oval nuclei (fig. 67) not very different from those of the hypodermis. Like the cells of the hypodermis also, they show no separating boundaries, nor have I seen any evidence of a basement membrane, or surrounding thin layer of cells such as clothe the oviduct. That the sac cannot be glandular appears from the nature of the epithelium, and although no spermatozoa were seen in it, it seems to be a true *receptaculum seminis*. The duct is short, and shows no difference in structure from the sac.

Concerning ovigenesis little can be said further than that the young ova appear to be budded from, or crowded out of the ovarian epithelium, from which they are to be distinguished by their large clear nuclei with distinct nuclear membrane. In many, but not all, the nuclei appear large deeply staining masses of chromatin. In most of the younger ova, masses of a similar appearance, but of a different tint, are to be found among the deeply staining cytoplastic granules. In more mature ova these masses disappear, and later, spherical yolk granules begin to form. In the most mature stages these constitute the greater central mass of the ovum, and are surrounded by a thin deeply-staining, finely-granular layer, forming the vitelline membrane.

THE MALE GENITAL SYSTEM.

The male sexual organs of *Pauropus* are of considerable interest from certain somewhat unexpected peculiarities shown. But whether they are characteristic of the Pauropoda I am unable to say, since among the twenty or more specimens of *Eurypauropus* at my command, not a single male was found. Such, however, may be the case as regards general features,

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while decided differences may appear in many details, for even in different individuals of *Pauropus huxleyi* I find strangely marked variations in structure; and, it may be added, that my results do not coincide with those of Schmidt ('94), further than that he also finds considerable variation in the sexual organs of this animal.

In mature individuals the testis, or the groups of developing spermatozoa composing it, lies above the intestine from the fifth or sixth somite backwards to the anal segment. In one case (fig. 72), it was found distinctly divided into two masses, the anterior of which was only little more than half the size of the posterior part. In another (fig. 71) it was likewise divided, but whether completely so, certain tearing of my sections leaves me unable to decide. Apparently, however, the two parts were connected by a narrow neck. In this specimen the smaller portion was posterior. In a third case the testis was entire.

In a specimen with only eight pairs of legs there are to be distinguished at least three and possibly four completely separated divisions, one of which lies ventro-laterally with respect to the intestine, the others dorsally and dorso-laterally.

In the absence of embryological evidence, one can but speculate upon the cause of this seemingly anomalous position of the testis in an animal which, from other characters seems to belong to a group where the position of the sexual organs of both sexes is either ventral or ventro-lateral. Evidence derived from the position of the ovary, and from *Scolopendrella*, where a portion of both testis and ovary are often found above the intestine and the rest below, seems to indicate that in this case the spermatic areas were originally ventro-lateral and that they have secondarily been crowded to a position above the intestine. If such be the process of development, then the one ventro-lateral mass in the immature specimen mentioned means merely that the process has not been quite completed.

The segmented condition of the organ seems readily explicable from what is generally known of the origin of the gonadial anlagen and testes. In this case the fusion of the cœlomic pouches is not always complete throughout, and it is not always the same pouches that fail to unite. Further the development

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is not always, apparently, bilateral, for in the immature specimen mentioned, there is no spermatic mass on the left side of the animal corresponding to that opposite, unless it has already moved upwards and backwards and become fused with the mass above the intestine. A little study of the post embryonic stages of the animals would show definitely the manner of development, but from lack of material I have thus far been unable to undertake it.

The epithelium of the testis is composed of a single layer of cubical cells without an outer supporting membrane or surrounding cellular layer other than that formed by the large cells of the fat-body. In some places it is filled with a solid mass of cells not unlike those of the epithelium. At others only small spermatozoidp cells are to be seen, while in others there may be distinguished other cells of different sizes grading between the epithelial and the spermatozoid cells (fig. 79). Some of the smaller cells are so grouped as to indicate their recent formation, and suggest the manner of development of the spermatozoa.

Leading from the sperm masses there may be at least three distinct small and short tubes (figs. 72, 80, 71,) often very difficult to follow through the various sections. These *vasa deferentia* do not all correspond in position in the two individuals studied most thoroughly. In one, two tubes arise from the anterior sperm mass, but not opposite one another, while one is given off from the left side of the posterior mass. In the other specimen all three arise from the anterior mass, one on the left side of the forward end, the other two, nearly opposite each other, from the hinder end.

Each *vas deferens* communicates with the end or side of a large tube, of which there may be several forming a complicated system of *vesciculæ seminales*. These form long tubes along the side or below the intestine and bend upon themselves, forming kinks, or anastomosing with one another into a mesh or loops. Their diameter and the appearance of their epithelium varies with the degree of distention by masses of spermatozoa. Where distended the epithelium is little more than a thin nucleated membrane, while in places where the sperm masses are absent, the cells are nearly cubical and the lumen proportionately small (figs. 75, 76, 77). The form and numbers of these tubes varies

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greatly. In one case (fig. 72) four long tubes were found, one of which (2) was not connected with the testis and formed a large loop at the end. In another (fig. 71) there were but two long tubes. From these, branches arose, which anastomosed in a peculiar manner.

But, however many *vesciculæ seminales* there may be, they all become united anteriorly, though, as may be seen from the figures, not in the same manner in two individuals, and communicate with a tube of small diameter or *ductus ejaculatorius posterior communis* (figs. 72 and 71 *depc* and 74). After a short distance, or at about the middle of the fifth segment, this gives off a short branch to the right, (*depd*) which may therefore be termed the *ductus ejaculatorius posterior dexter*, providing a Latin name be really necessary.

Lying on the right and the left side of the body, between the nerve cord and the intestine, and passing through the fourth segment are two large glandular ducts, *ducti ejaculatorii glandulares*, with a very high epithelium and very small lumen (fig. 72, 71*deg.* and 73). Posteriorly these fuse with the *ducti ejaculatorii posteriores* of their respective sides, while from the under side of their anterior ends a small duct passes from each down around the side of the nerve cord to an external opening on the corresponding side of the mid-ventral line, and just back of, but nearly between, the second pair of legs. These are the *ducti ejaculatorii anteriores.* Communicating with each is a small pyriform *glandula accessoria*, and externally a small penis, noticed as such by Lubbock in *Pauropus* and by Latzel in *Eurypauropus ornatus* (fig. 12).

Whether these small structures are in reality penes, my sections do not enable me to say with certainty, but apparently the ejaculatory ducts open through them, and both Lubbock and Latzel were able to distinguish a small canal in each. They are not unlike the penes of *Polyxenus* (fig. 19).

As already intimated, my results are far from being in accordance with those of Schmidt. He does not seem to have found a segmented condition of the testes, nor more than two vasa deferentia. Relative to the latter and to the tubes with which they connect, he says: "Ungefähr in seiner (Testikel) Mitte

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gehen von seinen Seitenwänden zwei enge vasa deferentia ab, die sogleich in zwei schlauchförmige, nach hinten verlaufende, doppelte Vesiculæ seminales einmunden. Die Vesiculæ seminales liegen zu beiden seiten des Darmcanals und jeder obere Schlauch ist mit dem unteren durch 1 2 Anastomosen verbunden; sie scheinen aber ihrer Form und der Einmundungsstellen der Vasa deferentia nach höchst inconstant zu sein."

"In dem vorletzten Segmente münden die Vesiculæ seminales in 2 ebenfalls schlauchförmige aber nach vorn verlaufende Ducti ejaculatorii posteriores ein, die ungefähr ein VI. Segmente sich verdoppeln in dem IV. aber alle vier sich durch einen quer verlaufenden Verbindungscanal zu einen unpaaren Duct. ejac. post. communis vereinigen."

Since my studies show such decided variations in different individuals, this account simply shows further evidence of the same. There may be two or three—and one would not be surprised to find four or five—vasa deferentia. But while we are agreed as to the anastomosing of the other ducts, I find no evidence for distinguishing them as vesiculæ seminales and ducti ejaculatorii posteriores. What Schmidt describes under those names are, according to my sections, one and the same thing. His figure shows the former as large anastomosing tubes with thin walls and the latter with thick walls. In my description I have pointed out that the difference in the thickness of the walls is due to the presence or absence of masses of spermatozoa. In none of my sections can I find any real histological difference between the hinder and the forward part of these tubes. The whole, from the vasa deferentia to the ductus ejaculatorius posterior (mihi) are vesiculæ seminales.

Whether these have an ectodermal origin or result from the fusion of cœlomic pouches—a view by which their irregularities is probably most readily explained,—and whether all these vasa deferentia are morphologically such *sensu strictu* cannot of course be affirmed in the absence of ontogenetic data. Certainly the latter are functionally vasa deferentia, and whether any of them are secondary or late formations from the testis, or persisting cœlomic diverticulæ matters little, for it amounts to nearly the same thing. The anomalous condition of more than two

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such ducts does not, however, appear so peculiar when one considers that Wheeler ('93) finds that two pairs of ducts develop in *Xiphidium*. The most important matter is the variation in position, which seems to show that almost any cœlomic diverticula may persist.

It may be remarked that in the one immature specimen sectioned, I saw no vasa deferentia. This, however, may be explained from the difficulty in distinguishing them even in the mature animal, where the vacuolation of the cells of the fat body and the manner in which these take up a stain makes following of all the small ducts a very pains-taking process.

Further differences appear in our results relative to the anterior portion of the system. Schmidt says: Es dringen in die Ruthen 2 Ducti ejacul. anteriores ein, die oben in die glandulæ accessoriæ münden. Die firnförmigen glandulæ aber sind hinten durch einen Duct. ejacul. anter. communis verbunden, in welcher der obengenannte Duct. ejac. post. communis mündet." Here it will be noticed that the glandulæ accessoriæs mihi and the ducti ejac. glandulares have been confounded. From Schmidt's figure it appears either that there are no ducti ejac. anteriores, such as I have described as running around the side of the nerve cord, or that they are very short, and further, that his duct. ejac. ant. communis lies below the nerve cord. As I find no evidence of a duct crossing the body

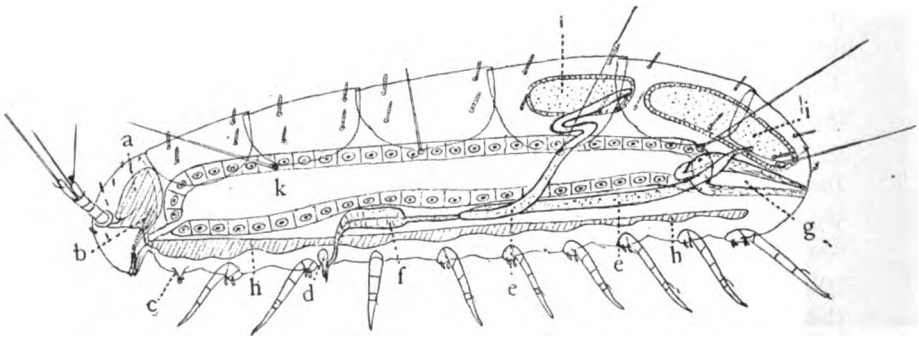

DIAGRAM II. THE MALE PAUROPUS; *a*, brain; *b*, Salivary gland; *c*, bud-like remnants of coxæ; *d*, penis; *e*, vesicula seminalis; *f*, ducters glandularis; *g*, rectum; *h*, ventral nerve cord; *i*, divisions of testes.

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below the nervous system, this duct must be what I have described as a branch, and his glandulæ accessoriæ close to which it is figured must be my ducti ejac. glandulares. Certainly the glands shown in his figure are much too large, although they are in the same position, to be the small pear-shaped glands that I find. (See, Appendix.)

THE DEVELOPMENT OF PAUROPODA.

What little is known of the development of the Pauropoda can be shortly told. Like the better known diplopods the young escape from the egg with three pairs of legs, after which they pass through four successive stages before attaining the nine leg-pair or adult condition. Of the stages in *Pauropus huxleyi* all have been seen, but not all fully and accurately described, while in *Eurypauropus* only the first, third and fifth stages have been observed.

Lubbock describes the newly hatched *Pauropus* as being $\frac{1}{72}$ of an inch in length, bearing three pairs of legs, three large dorsal plates, and two lateral hairs, and having consequently, according to my enumeration, six body segments (fig. 14). To quote verbatim "The first pair [of legs] was attached to the third segment (i. e. the one immediately succeeding the head), the other two to the following one. Beyond the legs were two other segments, making six in all, as seen from above, and counting the head as two. The fourth and fifth segments each bear a pair of long bristles, as in the grown animal." Latzel also has seen the hexapodial *Pauropus* and likewise the later stages.

Development appears to proceed slowly, for Lubbock mentions having collected a hexapodial animal on the 24th of October, which up to the time of its death, on the 6th of December, had undergone no change whatever. But finally, as seen by the same observer, a molting time does come; the animal leaves its old cuticle and appears with five pairs of legs, another pair of lateral hairs and one additional large segment, or with eight body segments in all. This stage may be further described as having only two joints in the basal portion of the antennæ.

There is then no stage with only four pairs of legs. The attainment of legs in groups of two pairs, however, ends with the

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second stage. In all the rest only one pair appears at a molt. In the third stage there are six pairs of legs, three basal antennal joints, five dorsal plates, four pairs of hairs, and nine body segments. In the next stage there are seven pairs of legs, and probably four pairs of lateral hairs, five dorsal plates and nine body segments, judging from what appears in the five leg-pair stage. The facts in the case I have not had an opportunity to learn. In the last postembryonic stage there are eight pairs of legs, while the hairs, plates and segmentation are as in the adult.

From this it appears—and stained toto preparations of mine show it—that the germinal area lies in the penultimate segment.

In *Eurypauropus* Ryder ('79) saw the individuals in the first or hexapodial stage (fig. 7), which he describes thus: "The larval *Eurypauropus* is exceedingly depressed, more so relatively than the adult, and appearing on this account very much like a young *Cimex* or bed-bug," and as having three or possibly four segments, and two pairs of lateral hairs, of which the posterior are terminally clavate. In the segmentation he of course, as already pointed out, mistook the first dorsal plate, beneath which the head and first body segment are withdrawn, for the head segment. Allowance being made for this mistake, the hexapodial *Eurypauropus* is not different from the same stage of *Pauropus*. The apparently anomalous condition of the three pairs of legs, i. e., all belonging to one segment as indicated by the middle dorsal plate in Ryder's figure, is readily explained by the manner in which the head and anterior segments are pushed backwards ventrally. Or, possibly the figure is not quite true to nature.

Of the other stages Latzel has seen a *Eurypauropus spinosus* with six pairs of legs, six dorsal plates and four pairs of lateral hairs, of which the third pair is clavate as in the adult, and a *E. ornatus* with eight pairs of legs and with the segments and hairs as in the mature animal.

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CLASSIFICATION OF THE PAUROPODA.

From many peculiarities of structure the Pauropoda are, as assumed in discussing their anatomy, undoubtedly Diplopoda. As in the Diplopoda the genital aperture occurs upon the third post cephalic segment, the ovary is below the intestine, the mouth parts are composed of a pair of mandibles and of a lower lip. The intestine is simple, with no strongly developed muscularis in the middle portion; there are two Malpighian tubes (when present); a portion of the body segmentation is double or strongly tends to be so; the legs are six jointed; the cuticle is thickened and covered with spines (in one case); the dorsal plates are ornamented with one or two transverse series of hairs or protuberances; the food habits are apparently not essentially different, and the movements are slow.

All these characters certainly outweigh the apparently anomalous position of the testes, the cleft antennæ and thin flagella, the more or less simple segmentation, the quick movements in *Pauropus*, and the lack of tracheal and circulatory system.

But, if their relation with the Diplopoda as a group is readily determined, their correct position within the group is far less so. That they are primitive in some respects, is shown by the simplicity of the segmentation, which, in fact, seems to throw considerable light upon the segmentation so peculiar to the Diplopoda; that they are degenerate is equally well demonstrated by the lack of tracheal and circulatory systems. Such facts completely exclude them from any very close relationship with any of the juloid or glomeroid forms; and this conclusion is further borne out by the structure of the nerve cord, the distribution of its ganglionic cells, the fusion of the anterior ganglia, and the structure of the brain with its enormous frontal lobe. On the other hand, while the characters that have vaguely re-called to the minds of other observers, the hairy and peculiar *Polyxenus*, are nothing more than superficial, these supported by a very striking similarity in the structure of the brain, the

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ventral cord, and in the fusion of the sub-œsophageal and anterior ganglia, and the similarity in the so called penes, all imply a relationship with this form, that certainly is much closer than with any other member of the Diplopoda.

But even here the relationship is not so very close, or nearer than a subordinal degree, even if it may justly be said to be as near as that. *Polyxenus* is a very much more highly organized animal than the Pauropoda; it possesses well developed circulatory and tracheal respiratory systems, well developed sense organs, a complex oral structure, and typical diplopod antennæ. In its manner of development, it likewise shows an important difference. In Pauropoda the appearance of the leg-pairs in the different stages may be represented as follows, 3, 2, 1, 1, 1, 1 (=9), while in *Polyxenus* the sequence is, 3, 1, 1, 1, 2, 2, 2, 1 (=13).

From these facts I am, I think, justified in reducing the Pauropoda from the ordinal position that they have hitherto held to that of a sub-order, forming along with its companion sub-order Pselophognatha, an order that may be termed the Protodiplopoda—for they seem to have retained the original unisegmental condition to a much greater extent than any other group of Diplopods. They doubtlessly arose gradually from the primative more vermiform Diplopoda along with those of which *Glomeris* is a type (Oniscomorpha of Pocock), but from these they became early and widely separated.

ORDER PROTODIPLOPODA.

SUB ORDER PAUROPODA.

Ord.	Pauropoda,	Lubbock.	Trans. Linn. Soc. XXVI, 1866, p. 185.
"	"	Ryder.	Amer. Nat. XIII, 1879, p. 603.
"	"	Latzel.	Myriopoden d. österreichisch-ungarischen Monarchie, Part II, 1884, p. 18.
"	"	Bollman.	Bulletin 46, U. S. Nat. Mus. 1893, Myriapoda of No. America, p. 162.

"Heterognathes, Saussure et Humbolt (teste Latzel). Mission scient. au Mexique, 1872, VI, 2 sect., p. 8,

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Body with twelve segments, eight of which tend to fuse into four double segments; nine pairs of legs, or the first, and the penultimate and anal segments apodial; first and anal legs five jointed, the rest six jointed. Head with a pair of mandibles and with a pair of maxillæ more or less fused into a lower lip; antennæ with a basal portion consisting of four joints, the fourth bearing at its apex two small joints, the smaller of which (stylus angustior) bears a long, ringed, flagellum and the larger (stylus latior) two such flagella; between the flagella of the stylus latior a globular body (globulus), stalked or sessile. Without tracheæ or a vascular system; subœsophageal ganglion and ganglia one and two of the ventral cord fused into a single mass; brain with two cerebral, or upper, two antennal lobes, and a large median unpaired frontal lobe, behind which is a small cleft through the brain mass. Ovary lying below the intestine, oviduct showing a posterior glandular and an anterior simple duct-like portion; a single *receptaculum seminis;* testes lying above the intestine, with two or three *vasa deferentia*, and a system of irregularly fused, long, *vesiculæ seminales*, a small *ductus ejaculatorius posterior communis*, two *ducti ejaculatorii glandulares*, a connecting *ductus ejaculatorius posterior dexter*, two *ducti ejaculatorii anteriores* and two pyriform accessory glands. Genital openings in the third body segment between and a little behind the second pair of legs. The female genital aperture unpaired and to the right of the median line; the two of the male paired. Malpighian tubes two or wanting; cells of the mid-gut filled with crystals.

ANALYSIS OF THE FAMILIES.

1. Pauropoda with six dorsal plates, and four more or less completely formed double segments.

   a) Pauropoda with long, rounded bodies, long legs, and agile movements.

   Pauropodidæ.

   b) Pauropoda with depressed bodies, thickened cuticle, short legs and slow movements.

   Eurypauropodidæ.

2. Pauropoda of uncertain position, with ten dorsal plates.

   Brachypauropus Latz.

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Pauropodidæ Lub.

Pauropodidæ,	Lubbock,	Trans. Linn. Soc. XXVI, 1866, p. 185.
"	Ryder,	Amer. Nat. XIII, 1879, p. 610.
Pauropoda agilia,	Latzel,	Verhandl. d. zool.-bot. Ges. Wien, XXXIII, 1883, p. 127. Myriopoden d. österreichisch-ungarischen Monarchie, Part II, 1884, p. 21.
Pauropodidæ,	Bollman.	Myriapoda of North America, Bull, U. S. Nat. Mus. 46, 1893, p. 162.

Body long, rounded; head free, or not hidden; cuticle thin; six large dorsal plates, each with two transverse pairs of clavate ringed hairs; these larger anteriorly, becoming larger and less clavate posteriorly; similar hairs on the head and antennal joints; with two supra-anal, apparently jointed, short styliform hairs; five pairs of lateral tactile hairs, a pair near the anterior angle of the second dorsal plate, a pair in front of the middle of the margin of the third, near the middle of the fourth, behind the middle of the fifth, and near the posterior angle of the sixth plate; legs long, increasing in length posteriorly; movements agile, letusimulates only when severely teased; Malpighian tubes wanting (*P. huxleyi*); the second, third, fourth, and fifth dorsal plates tending to form, with the underlying eight pairs of legs, or with all but the first pair, four double segments.

Found throughout Europe and in Eastern North America.

PAUROPUS LUB.

Pauropus,	Lubbock,	Trans. Linn. Soc. Lond. vol. XXVI, 1866, p. 181.
"	Ryder,	Amer. Nat., vol. XIII, 1879, p. 611.
"	Latzel,	Myriapoden d. österreichisch-ungarischen Monarchie, part II, 1884, p. 22.

Body somewhat elongate, increasing in size posteriorly, the fourth and fifth dorsal plates largest; penultimate legs longest; lateral tactile hairs, long linear; seen under high magnification, very finely plumose distally; two transverse rows of clavate,

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ringed hairs upon each dorsal plate; the inner and outer branch of the hypopharyngeal framework of equal length, their anterior halves fused or in contact; the globulus stalked or sessile.

This genus is of interest in having been the first of the group discovered and from the manner of its reception, Lubbock considering it a synthetic animal breaking the monotony of the Myriapoda and connecting not only the Diplopoda and Chilopoda, but also these with insects and Crustacea. Very soon after its discovery, Packard made use of the hexapodial young in speculating upon the origin of insects. But, to say nothing of its very anamalous male genital system, it seems most interesting as affording, in the relation of its dorsal plates, pleuræ, and mode of growth, a possible clue to an explanation of diplopod segmentation.

It is with truth that Lubbock describes it as a "neat, active, little creature, and at first sight certainly looks like a Chilopod." He, however, compares it with *Lithobius*, but its actions, and its rather long legs remind me more of *Scutigera*. It will run a little ways, then stop a moment and be off again. Its little eighteen legged body is nearly always comparatively straight. When teased excessively with the point of a fine needle, according to Ryder, it will roll up into a small ball and letusimulate. Just what its food may be is a mystery; its great agility as mentioned by Latzel would possibly indicate predaceous habits, but its oral structure is not very different from that of the slow-moving *Eurypauropus*. What is found in the intestine offers no clue, unless it be the crystals, which seem to me to possibly indicate that, like earth worms, chilognaths and some other low forms, it feeds upon humus. But whether it is predaceous or not, it itself has many enemies, some of them small mites. According to Latzel, "Sie selbst fallen anderen Thieren zur Beute. Einmal sah ich, wie eine weisse, robuste Milbe einen Pauropus tödtete und herumschlepte; sie liess ihn mehrmals fallen, lief um ihn herum, packte ihn von Neuem und lief dann davon mit ihm."

The only two species of the genus are readily distinguishable from one another as follows:—

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1. *Stylus latior* and *angustior* sub-equal in length; *globulus* stalked, flagelli of the *stylus latior* unequal.

P. pedunculatus Lub.

2. *Stylus latior* a little more than half as long as the *stylus angustior*; its *flagella* sub-equal; *globulus* sessile.

P. huxleyi Lub.

Pauropus Huxleyi Lub.

Pauropus huxleyi,	Lubbock, Trans. Linn. Soc. Lond. XXVI, 1866, p. 182.
" "	Ryder, Amer. Nat. XIII, 1879, p. 611.
" *lubbockii*,	Packard, Proc. Boston Soc. Nat. Hist. XIII, p. 409. Amer. Nat. IV, 1871, p. 621. Ann. and Mag. Nat Hist. 4th ser., VII, p. 72.
" *huxleyi*,	Latzel, Myriapoden d. österreichisch-ungarischen Monarchie, part II, 1884, p. 23.

Faintly yellowish, nearly white; body slender, tapering anteriorly; flagella of the stylus latior sub-equal, inner one shortest, bulb arising from the tip of the stylus; flagellum of the stylus angustior as much longer than the middle flagellum as this is longer than the inner. Stylus latior of larger diameter, and a little more than half as long as the stylus angustior. Globulus small, sessile or sub-sessile. Fifth dorsal plate largest, seventh smallest; all the plates smooth, each with two transverse rows of clavate, ringed hairs; these largest anteriorly, less clavate posteriorly; similar hairs on the head and antennæ, the latter with long, tapering hairs also. Lateral, tactile hairs long, tapering, very delicately and shortly plumose distally, ringing obsolete basally, fifth or last pair longest. Legs increasing in length posteriorly, penultimate longest; feet with a single median large claw and two opposite smaller claws at right angles to it, with an oval adhering disc between them. Malpighian tubes wanting; sexual organs as described for the order. Length of body, 1—1.3 mm.; width, .2—.35 mm.

Found in England, Austro-Hungary, near St. Petersburg, in Eastern Massachusetts, (Salem, Chelsea, Boston) and at Philadelphia.

St. Petersburg is given upon the supposition that Schmidt

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('94) obtained his anatomical material in its neighborhood.* Salem and Chelsea are the localities where Packard's *P. lubbockii* was found. But this can be nothing else than *P. huxleyi* so far as one can judge from the very poor description, the only distinctive features mentioned being the nearly equal length of the flagella. This is in truth different from Lubbock's figure, but since, in animals taken in middle Europe, Latzel describes the flagella as I have found them in animals taken here near Boston, there is some likelihood of the figure not being quite true to nature.

Pauropus Pedunculatus Lub.

Pauropus pedunculatus,	Lubbock, Trans. Linn. Soc. XXVI, p. 185.
" "	Ryder, Amer. Nat. XIII, 1879, p. 611.
" "	Latzel, Myriapoden d. österreichisch-ungarischen Monarchie, part II, 1884, p. 27.

Larger than *Pauropus huxleyi*, antennæ very different, otherwise very closely similar. Stylus latior and angustior sub-equal in length, the latter smaller in diameter, inner and outer flagella sub-equal, both placed apically on their styli; middle flagellum much the shortest, arising from the side of the stylus. Globulus upon a stalk arising from the side of the stylus above the origin of the middle flagellum. Flagella with only a very short unringed basal portion. Length 1.5 mm. width, .4 mm.

Found in England, Carinthia (Latzel) Breslau (Haase)†. Not common.

Eurypauropodidæ Ryder.

Eurypauropodidæ,	Ryder, Amer. Nat. XIII, 1879, p. 611.
Pauropoda tardigrada,	Latzel, (*Partim*), Verhandl d. zool.-bot. Ges. Wien. XXXIII, 1883, p. 127. Myriapoden d österreichisch-ungarischen Monarchie, part II, p. 28.

*In his later, or final paper, Schmidt gives St. Petersburg and Norway as places where he has found this species. See Zeitsch. f. wiss. Zool. LIX, p. 438.

†This species has been found also at St. Petersburg, by Schmidt, v. l. c. p. 120.

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Eurypauropodidæ, Bollman, (*Partim*) Myriapoda of North America, Bull. U. S. Nat. Mus. 46, 1893, p. 162.

Body depressed, arched, ellipsoidal in outline; with six large dorsal plates variously ornamented with spines or wart-like protuberances or both; the legs behind the first pair in groups of two pairs, forming, with the second, third, fourth and fifth dorsal plates, double segments as in Chilognatha; legs short, in life, scarcely, if at all, projecting beyond the margin of the body, their segmentation and claws as in *Pauropus*; head concealed beneath the large anterior dorsal plate, but capable of being crowded out in front of the plate; body segments as indicated by the dorsal plates, (the head with the first real segment being concealed,) apparently only seven; five pairs of tactile hairs arising from the pleuræ, a pair at the anterior angle of the second dorsal plate, in front of the middle of the edge of the third, near the middle of the fourth, behind the middle of the fifth, and at the posterior angle of the sixth. Motions slow; letusimulates habitually. Malpighian tubes two (*E. spinosus* ♀).

One genus composes the family, all the species of which have been found in Europe, but only one in America.

Both Ryder and Latzel have been struck with some polyxenoid features in these animals. Ryder compared the spines of *E. spinosus* with the deciduous hairs of *Polyxenus*. Latzel speaks of the general appearance as reminding him of a *Polyxenus* or young *Polyzonium*. There are, in fact, many external and some internal features common to them.

EURYPAUROPUS RYDER.

Eurypauropus, Ryder, Amer. Nat. XIII, 1879, p. 603.
" Latzel, Vorhandl. zool.-bot. Ges. Wien. XXXIII, 1883, p. 127. Myriapoden d. österreichisch-ungarischen Monarchie, part II, 1884, p. 32.

With the characters of the family and with the stylus latior longer than the stylus angustior and the globulus upon a long peduncle, the three known species may be readily distinguished from one another as follows:

1. Without raised lines on the dorsal plates, none of the tactile hairs plumose, third pair clavate.

E. spinosus Ryder.

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2. With raised lines on the dorsal plates.

a) Dorsal plates without hooked spines, but thickly covered with wart-like protuberances; no connecting raised lines enclosing small sunken areas; third pair of tactile hairs short, clavate and plumose.

E. cycliger Latzel.

b) Dorsal plates with hooked spines on raised longitudinal and connecting lines enclosing depressed areas without such spines, third pair of tactile hairs not clavate.

E. ornatus Latzel.

Eurypauropus spinosus Ryder.

Eurypauropus spinosus, Ryder, Amer. Nat. XIII, 1879, p. 603. Fig. I-VIII, p. 605, I-II, p. 610. Proc. Acad. Nat. Sci. Phil., 1879, p. 139, p. 164.
Latzel, Myriapoden d. österreichisch-ungarischen Monarchie, part II, 1884.

Light to dark reddish brown above, pale below; flagellum of the stylus angustior considerably longer than the other flagella, of which the inner is the shorter; peduncle of the globulus clavate, long, half the length of the stylus; the dorsal plates covered with short recurved hook-like spines, between these, with numerous low, conical processes connected with one another by a series of lines giving the appearance of a triagonal and hexagonal meshwork; dorsal spines flattened on top, marginal ones more truly spine-like; lateral, tactile hairs projecting upwards through small notches in the margins of the dorsal plates, third pair short, with a clavate termination. Length, .9—1.25 mm., width, .45—.5 mm.

Found at Fairmount Park, Philadelphia, Williamstown, Mass. and by Latzel in Carinthia. Of the young of this Ryder saw two specimens in the first post-embryonic stage with three pairs of legs, three large segments indicated by three large dorsal plates and a possible fourth small anal segment, and with two pairs of tactile hairs of which the hinder pair were clavate. Latzel found young 0.5 mm long with six pairs of legs, six dorsal plates and four pairs of tactile hairs of which the third pair, as in the adult, were clavate.

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Eurypauropus cycliger Latzel.

Eurypauropus cycliger, Latzel, Verhandl. d. zool.-bot. Ges. Wien. XXXIII, 1883, p. 127. Myriopoden d. österreichisch-ungarischen Monarchie. Part II, 1884, p. 37.

Similar to *Eurypauropus ornatus* and *spinosus*, but of a rust-brown color, and with the dorsal plates covered with conical processes arranged in circular groups or rosettes in irregular transverse rows; the hinder protuberance of each group with a short bristle; no spinous processes; no raised connecting lines, but with two longitudinal raised right and left lines; these united anteriorly; the third pair of tactile hairs shorter than the rest, clavate and finely plumose. Length, .8—1 mm., width, .4—.6 mm.

Of this species Latzel found five individuals, one in lower Austria along with *Eurypauropus ornatus*, the others in Carinthia with *E. spinosus*.

Eurypauropus ornatus Latzel.

Eurypauropus ornatus, Latzel, Verhandl. d. zool.-bot. Ges. Wien. XXXIII, 1883, p. 127. Myriopoden d. österreichisch-ungarischen Monarchie. Part II, 1884, p. 34. Plate II, figs. 13-21.

Brown or sub-ochreous, pale below; stylus latior somewhat shorter than the stylus angustior, flagella sub-equal in length, inner shortest, outer longest; peduncle of the globulus more than half the length of the stylus, straight, swollen in the middle; dorsal plates with raised longitudinal lines, and raised cross connecting lines, so that the first plate shows eight, the second, third, fourth and fifth, five, and the sixth two depressed areas; hook-like spines on the raised areas only; depressed areas with wart-like protuberances; tactile hairs all tapering, or none clavate. Length, 0.9—1.3 mm., width, 0.45—0.6 mm.

Of the younger stages Latzel found only that with eight pairs of legs, which is otherwise not unlike the adult.

Concerning the habitat and distribution of this interesting form Latzel says:—"Die Thierchen sitzen, im Gegensatze zu dem

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agilen Pauropus, ganz ruhig an der unterseite der Steine, welche an etwas abschüssigen Stellen feuchter, bewaldeter Schluchten, am Rande von Hohlwegen u. s. w. liegen oder mehr weniger bemoost sind. Gewohnlich findet man nur ein einselnes Individuum, seltener unter demselben Steine drei bis vier oder gar fünf bis acht solche Thierchen. Dagegen kann man wieder viele Dutzende Steine ganze umsonst auf Eurypauropus untersuchen, so dass man diese Thierchen wohl als ziemlich selten bezeichnen kann. Ob sie auch faulendem Holze leben, wie die amerikanischen Formen, ist mir nicht bekannt. Wohl aber glaube ich vermuthen zu dürfen, dass sie nicht bloss auf einzelne Gegenden Niederöterreichs beschränkt sind, sondern wahrscheinlich im ganzen Alpengebiete auftreten dürften."

Pauropoda of uncertain position.

Brachypauropus hamiger latzel.

Brachypauropus hamiger, Latzel, Myriopoden der österreichisch-ungarischen Monarchie. Part II, 1884, p. 28-32.

Although in certain respects this appears to be closely related to *Eurypauropus*, the anomolous number of the dorsal plates is a characteristic of such value as to exclude it from the same family. It is far more primitive than *Eurypauropus* and may possibly be closely similar to the ancestral form of that genus. But not being able personally to study the animal, I do not feel warranted in erecting a third family for it, though judging from Latzel's description, I am very strongly inclined to believe that a family Brachypauropodidæ will eventually prove necessary in order to express properly the relationships of the animal. There will then also be needed a super family with slow movements for its chief characteristic. For such a super family the short and expressive term Tardimota may be employed, while the contrasting group may be known as the Agilimota.

Latzel's description of the genus is as follows :—"Der winzige Körper ist im lebenden Zustande fast kegelförmig verkürzt, im todten Zustande länglich eiformig, niedergedrückt bis mässig gewölbt, scheinbar von zehn (endlich veilleicht von eilf) Rück-

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enschilden bedeckt, welche nahezu dieselbe Grösse zeigen, sehr mässige Chitin-Einlagerungen und wenig vorspringende Sculptur besitzen; dagegen sind sie mit kräftigen Haargebilden besetzt. Der zweite und dritte Rückenschild, ebenso der vierte und fünfte, sechste und siebente, achte und neunte können je paarig einander genähert sein. Denkt man sich diese Paare verwachsen, so resultiren sechs, beim geschlechtsreifen Thiere wahrscheinlich sieben Rückenschilde, wie bei den Gattungen Pauropus und Eurypauropus. Eine seitliche Randbewaffnung gewahrt man an den Rückenschilden nicht; die seitlichen Haargebilde, welche die Basis der sehr feinen, mässig langen Tasthaare umstehen, scheinen mit diesen bereits unter dem Schildrande in den Pleuren zu sitzen, und zwar jederseits am 2. 4. 7. 9. (10.) Segmente des Körpers. Der sehr kleine Kopf verbirgt sich nicht unter dem ersten Rückenschilde. Die Pleuren bleiben ganz frei, resp. unbedeckt, wenn sie auch durch Chitin-Einlagerung die beginnende Verschmelzung mit den Rückenschilden (wie bei Euryp.) andeuten."

Further than this the genus and species may be described as having the dorsal plates broader than long, the first possessing eight yellow spines in two transverse rows, of which the first turn anteriorly, the second posteriorly, and each of all the remaining plates with four spines pointing posteriorly and in one transverse row; long antennæ with the stylus angustior shorter, but only a little smaller than the other, one of the pair of flagella on the stylus latior a little shorter than the other, and the globulus on a stalk relatively shorter than that in *Eurypauropus ornatus* or in *Pauropus pedunculatus*. Length, 0.4 mm., width, 0.2 mm.

Latzel found animals with six with twelve and with sixteen legs. Hence the adult has apparently not been seen. Of these the animal with six pairs of legs possessed nine dorsal plates and four tactile hairs, and that with three pairs of legs, seven dorsal plates and three pairs of lateral hairs. Out of twenty-five specimens collected only ten were studied.

Concerning their habitat Latzel says: "Ich fand sie alle an einem und demselben engbegrenzten Orte, nämlich in Kärnten, im Mittelgebirge zwichen Klagenfurt und dem Wörthersee. Sie

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leben an feuchten, unter Torfmoos verborgenen Steinen, welche mit Erde und Schutt die Böschung von nordseitigen, bewaldeten Berglehnen und Hohlwegen bilden. . . . . Um sie im unversehrten Zustande zeichnen zu können, müsste man im Walde, an Ort und Stelle das Mikroskop aufstellen; denn bevor man sie von Steine abgehoben nach Hause bringt, sind sie stark lädirt. "

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NOTES ON THE MORPHOLOGY OF DIPLOPODA.

In the first half of the present century when the idea of evolution was dormant, but some years before it had startled the firm believers in the immutability of species, we find Newport ('41) describing the diplopods as being nearer the worms in the simplicity of their nervous system and of their alimentary canal, and in the form of the body, than the Chilopoda, which in many respects he regarded as standing close to Hexapoda. In the laws that he pointed out and in his explanations of peculiarities of structure he showed much better judgment than many a later naturalist with the better opportunities of greater knowledge and of the established evolutionary theory. In his excellent monograph "On the Organs of Reproduction, and the Development of the Myriapoda" he states that "The true Insecta arrive at their perfect state by an aggregation or apparent diminution in the number of their segments, but the Myriapoda, on the contrary, by a repeated increase of these parts, which in many instances are multiplied to several times their original number. This addition of segments during the growth of the animal, occurs throughout the whole class, and is one of its chief characteristics." Regarding the formation of the double segments he was much nearer the truth than Dana, Packard or Balfour when he supposed them formed by fusion rather than by splitting.

Over twenty years later this autogenetic law of elongation played an important part in Hæckel's brilliant and daring application of the theory of evolution to the whole animal kingdom. In the new phylogenetic method of classification here ushered in, the Myriapoda became genetically and closely connected with the hexapodial insect, for they and all other tracheates were supposed to have originated from a common hexapodial form which in turn was supposed to have developed from some ancient zoëa-like animal. And as regards the relation of the Chilopoda to the Diplopoda the latter were thought to have come from

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the former (Hæckel, '71), which possessed the more simple segmentation, a view which, as pointed out by Haase ('81), is without the support of paleontology, since diplopods occur in carboniferous, and, if the Archipolypoda of Scudder be admitted, as early as Devonian times, while no chilopods have been found in earlier than tertiary strata.

Hæckel's derivation of the tracheates from a crustacean form was criticised by, among others, Packard ('71) who went back to the older idea suggested by Newport's comparisons and derived the hexapods, and with them arachnids and myriapods from parapodia-bearing, or aquatic, worms, which, when they first emerged from the water had attained a form similar to the diminutive hexapodial larva of *Pauropus*. Somewhat later ('83), in treating of the Myriapoda particularly, he takes it for granted as did Hæckel long before, that the appendages, oral and otherwise of hexapods, chilopods and diplopods are homodynamous and homologous, and mislead by the hexapodial diplopod young, he says: "Looking at the embryo diplopod myriapod from a deductive or speculative point of view, it doubtless represents or is merely allied to what was the primitive myriapodous type of Tracheate with a cylindrical body, whose head, clearly separated from the hind body, was composed of three cephalic segments, one pair of antennæ succeeded by two post oral arthromeres, the protomalal and deutomalal arthromeres; while the hind body consisted of as few as seven arthromeres whose scuta nearly met beneath, with three pairs of six-jointed legs distributed among the first four segments. It is evident that the form represented by the adult is a later product and arose by adaptation to its present form." Here the Chilopoda are regarded as an offshoot of the Diplopoda, and the body segments of the latter as having later given rise to double segments by incomplete division. In this last supposition he does violence to the fact that nowhere in the whole group of arthropods is there definitely known a single instance of such a process, while numerous cases may be cited where fusion takes place. And, in the derivation of the Chilopoda, there is, as will be shown more fully later on, just as great a disregard of structural differences.

In 1881 Haase endeavored to derive the Chilopoda, Sym-

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phyla, and Thysanura from a symphyloid animal, basing his argument largely upon the manner of the development of *Lithobius* and Symphyla. But the perfection of the animal at the time of its escape from the egg, as shown in the development of hexapods and of other forms, is of secondary importance. In a later paper ('86) Haase changes and enlarges upon his earlier ideas by supposing the existence of an animal similar to *Peripatus* with as many segments as Symphyla and Pselphognatha, and with paired genital apertures at the hinder end of the body, and possibly, as suggested by Grassi, also between the third and fourth pairs of legs. In this, as in his earlier idea, the long-bodied Chilopoda developed according to the principle of elongation. From the same form also came independently the Symphyla, Diplopoda, and the ancestors of the Hexapoda.

About the same time Grassi expressed a view that hexapods and myriapods were intimately related and were to be derived from a campodean form, which in turn was to be derived from some crustacean. A year before Oudemans expressed doubts as to the naturalness of the group Tracheata, considering *Peripatus* as distinct and as possibly coming from gastrula-form animals with a nerve ring around the blastopore. The Hexapoda and Myriapoda he did not consider as derivable from the parapodia-bearing worms, and, while the embryology of these does not definitely point to their forming a natural group, the evidence from their anatomy is sufficient for their being classed as Insecta.

Pocock ('87) and Kingsley ('88) doubted the naturalness of the group Myriapoda, and later, Pocock ('93), laying stress upon the position of the genital apertures, derived the forms with anterior apertures, — Progoneata, — and those with posterior apertures, — Opisthogoneata, — separately from some primitive tracheate. The Pauropoda he considered as distinct from the Diplopoda, and supposed the Symphyla to have a common stem with the Chilopoda.

Von Kennel ('91) derived insects, arachnids and myriapods from a peripatiform group of animals which had arisen from the annelid worms. The Chilopoda he considered to have sprung from the hexapod branch, while the diplopod and symphylid

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branches arose independently from one that later gave rise to the arachnids. Pauropoda and Symphyla were supposed to have had a common origin.

In the same year Fernald, after studying the Thysanura, derived the Arthropoda from an unsegmented worm. But where the Myriapoda branched off he does not attempt to indicate. The Chilopoda, however, were supposed to have come off from the Diplopoda.

Recently the late J. D. Dana ('94) concluded that although there is no paleontological proof of a connection between worms and myriapods, such a connection is zoologically suggested. Further, he concluded that the myriapods are the precursors of the insects. But while this last supposition seems a very probable one, if by myriapods the chilopods should be meant, there seems to be in the paper a complete disregard of the facts presented by embryology and of the differences between chilopods, diplopods and hexapods. At the end of the paper one finds the astounding assertion that "the two pairs of maxillæ of insects are assumed to belong to a single body segment, as held by many zoologists."

If now the Diplopoda be compared with other members of the arthropodan group the tracheal system stands out prominently as formerly having been considered of great value; on the one hand in uniting terrestrial arthropods as Tracheata, and on the other in separating these from the Branchiata. But within the last fifteen or sixteen years it has been conclusively shown that the possession of tracheæ is of little morphological importance, since tracheæ may arise in several ways. First, Lankester ('81), then Kingsley ('85, '93) and others brought forward proof that *Limulus* is more nearly related to the Arachnida than to the Crustacea, Kingsley showing how the lung-books and probably the ventral tracheæ also of the spiders may have originated from the gill-books of this ancient animal. Then comes Simmons ('94) supporting Kingsley's idea with embryological evidence from a study of the early formation of the lung-books and tracheæ in *Agelena nævia* and *Theridium tepidariorum*, while Wagner ('94) shows that the tracheæ of mites are metamorphosed dermal glands, that they may occur almost anywhere on the body, and are hence of little value morphologically. One

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of the chief supports of the idea that Diplopda are genetically connected, either as being the original form or as being an offshoot of Hexapoda is therefore largely taken away, since greater weight is given to the differences that have been long known to exist. All that is left is the similarity in position of the stigmata. That, however, does not necessarily indicate a relationship closer than the annelidan worms.

This also holds good in a comparison of Diplopoda with Chilopoda. In the latter the branching tracheæ, with spiral thickenings of the intima so characteristic of the Hexapoda, contrast strongly with the smooth-walled, unbranching (except in *Polyxenus* and the Glomeridæ) tracheæ of the former group, and if a genetic relationship, such as that supposed by Hæckel or that supposed by Packard and others really existed, it becomes a somewhat difficult matter to show how the tracheæ of the one group may be derived from that of the other.

The character of the intestine, the Malpighian tubes, the circulatory system, the fat body and the nervous system offer as little of morphological value as the tracheal system, but what little there is contrasts the Diplopoda with the chilopods and hexapod insects, and at the same time brings them near the annelids. In the intestine there is no differentiation into the parts so easily recognized in Hexapoda, which were shown to be also present in Chilopoda by Balbiani ('90), Willem ('89) and others. While the ventral cord is exceedingly vermiform in the manner of fusion of the lateral halves and in the poorly developed ganglia, the eyes, given so much importance by Patten, show a structure that allies the diplopods with the arachnids rather than with the hexapods, if indeed they have anything more — which is not likely — than a homoplastic significance.

The so-called repugnatorial pores, however, are characteristic. Some of the chilopods, it is true, possess pores secreting a defensive fluid, but since such pores do not and cannot be made to coincide in morphological position they cannot be the homologues of the diplopodan organs. In the latter the organs occur as paired lateral, or unpaired dorsal, pores upon each double segment, while in the former they are upon the ventral surface of the animal.

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What they represent in the worms is an enigma if they are anything else than modified dermal glands. How they can have come from nephridia as held by Eisig is very difficult to see. The suggestion of Packard ('83) that they are comparable with coxal glands is even less worthy of support. Where they are dorsal as in the Glomeridæ they doubtless represent such dorsomedian glands as occur in *Lumbricus*.

The salivary glands also in their greatly elongated and simple form—especially if, as supposed by Heathcote, they are of mesodermal origin—differ decidedly from these organs in hexapods, while from those found in *Peripatus* they differ at least in the position of the segment to which they belong.

The ventral or coxal sacs, which are to some extent glandular, have justly, it seems, been compared with the coxal glands of *Peripatus* and the setiparous glands of annelids by Eisig ('87), and with the ventral sacs of *Scolopendrella* and Thysanura by Haase ('86).

Considering now the segmentation and appendages of Diplopoda, it appears that while the double nature of the body segments is so peculiar to the group, what little is known of the anatomy and development of the segments in the more common forms, as especially after what has been pointed out in connection with Pauropoda, together with the fact that in the Chilopoda there is (in *Lithobius*) a tendency, which seems completed in *Scutigera*, for the dorsal plates of alternate segments to become hypertrophied at the expense of all the other plates, goes to show that double segmentation does not necessarily separate diplopods from chilopods, nor even from hexapods. There is left, however, the disputed question concerning the segmentation of the head, which, according to those who have dealt chiefly with hexapods, is formed by the fusion of at least four segments, represented by antennæ, mandibles and two pairs of maxillæ. Here the reasoning is fallacious, since upon recognizing a head, thorax and abdomen in a highly developed form, it is thought that certain parts in a lower form must be cephalic, thoracic or abdominal; and where anything at all similar to one of these parts is found it is concluded that it must have the same construction. According to Huxley, Heathcote and Kingsley

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the so-called lower lip or gnathochilarium of diplopods is formed by the fusion of but one pair of appendages, which reduces the number of cephalic segments by one. Recently Kingsley ('94) has gone still further in regarding the bud-like processes belonging to the tritocerebral lobe—first recognized in the embryo bee by Bütschli ('70), then in the Lepidoptera by Tichomiroff, in *Meloe* by Nusbaum and more recently in Thysanura and Orthoptera by Wheeler ('93)—as the persisting remains of legs, a view that makes a still greater chasm between hexapods, chilopods and diplopods. But the same bud-like processes and the tritocerebral lobes are shown in Sograff's figure of the geophilid embryo, and, if Wheeler's suggestion be correct, that the transverse œsophageal commissure connects the tritocerebral lobes, it is probably true, since this or a similar commissure is found among diplopods, that this segment coming between the antennal and mandibular segments is not lacking in either chilopods or diplopods. Then, a protocerebral segment being indicated by the sensory lobes of the brain in diplopods as well as in other forms, there appears to be a difference of but one segment between the head of diplopods on the one hand and that of chilopods and hexapods on the other.

Only one strong blow has been given this idea, and that was by Haase ('81), who pointed out that in tenebrionid larvæ a lower lip occurs that is very closely similar to that of the Diplopoda. Later ('86) he says that the fusion of the two pairs of maxillæ has been so complete "dass sie schon am Embryo an einen Segment aufzutreten scheinen." Such a supposition as this is, however, entirely gratuitous. One would not expect from knowledge gained elsewhere that two pairs of appendages could not here be recognized as separate in embryonic stages, but should become so in the adult, for adult appearances do offer some ground to those who have regarded the gnathochilarium as formed of two pairs of maxillæ. And until evidence can be obtained from diplopod ontogeny of such a fusion the balance of evidence is decidedly in favor of the view of Huxley and Kingsley.

A similar problem is presented by the three pairs of legs with which the young diplopod escapes from the egg. In the Campodea theory these become thoracic legs, without regard to

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the fact that, even supposing the diplopod and hexapod head to be similar, the legs do not occur upon corresponding segments. For in the Julidæ there is an apodal segment between the second and third pairs of legs, while in Polydesmidæ the first post-cephalic segment is apodous. This difficulty cannot be surmounted by supposing, with Korschelt and Heider ('92) and others, that a segment has been intercalated. From the manner of growth of these and other arthropods such an interposition is impossible unless there should be a secondary division of a segment already formed. The interposition of a segment can be considered the true explanation only when the supposition that the three pairs of legs correspond to the hexapod legs is shown to be a fact. Until then it seems most plausible that the diplopod legs and segments have no genetic relations with those of hexapods, that a thorax is a thing peculiar to the latter, and that, applied to other forms, the term is a misnomer.

The sexual organs, which offer means of distinction much more important than any or all of the characters thus far discussed, remain to be considered. These in the Diplopoda lie beneath the intestine and open anteriorly to the exterior through paired openings on the ventral side of the third body segment. In *Peripatus*, chilopods and hexapods they lie dorsally and open at the posterior end of the body, and, as pointed out by Pocock, widely separate these groups from the rest of Arthropoda. The openings of the diplopods are too far forward to be explained by the Campodea theory and Haase's ('81, '86) principle of elongation, but are readily explained by supposing that there was once a time in the history of the Arthropoda when the sexual products set free in the body cavity might find egress through any or all nephridia, that these animals became divided into three groups, one in which the anterior, one in which the more median, and another in which the posterior nephridia took upon themselves the function of genital ducts. From the first came the diplopods, from the last the hexapods, chilopods and *Peripatus*, and from the second the mixed array of crustacean and arachnid forms.

Against such a view may be brought the fact shown by Wheeler ('93) that the male genital ducts of *Xiphidium* move for-

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ward in the embryo from the tenth to the ninth abdominal segments. His figures show that the terminal ampullæ of the ducts and the more anterior segments, at the stage when this change of position occurs, develop very much more rapidly than the anal and penultimate segments. As a consequence the ampullæ appear to be crowded forward so that they fuse with a ventro-median invagination of the ninth segment. There is no evidence that these paired external openings, comparable with those of nephridia, are here formed only to fuse later in the ventro-median line, and it is very probable that the unpaired ducts of insects and the ectodermal portion of nephridia are not homologous at all. What *Xiphidium* really illustrates, then, is that the ectodermal portion of the nephridial ducts has failed to develop, leaving the mesodermal portion to fuse with any other invagination that might occur.

This being the case, it is difficult to see just how conclusions drawn from primitive conditions are affected, and until such shifting of ducts can be shown to occur among diplopods and in other primitive forms, a phylogenetic classification based upon the position of the genital openings may be regarded as sound. That the male and female ducts may be homodynamous only, is here of minor importance, as is also the fact that in the female two pairs of ducts—one of which corresponds to the male ducts—are at first formed.

This question affects *Scolopendrella*, which has been so persistently looked upon as the possible ancestral form of other Antennata. The animal truly shows many chilopod and some thysanuran features, but until it can be shown from a study of its ontogeny that the genital ducts are already fairly well formed before the more posterior segments, it is safe to conclude that the position of the genital opening on the fourth body segment, oge ther with other characters, indicates an affinity nearer the Diplopoda than to any other group of arthropods. The median unpaired opening indicates a secondary formation arisen from the fusion of the outer portion of the nephridia of that segment, or, what is as likely, from an invagination entirely independent of them. The other characters of value are the mouth parts, ventral sacs, and ventral appendages. The first have been described as

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consisting of three pairs of appendages—except by Wood-Mason ('83), who thought the underlip comparable with that of Chilognatha. As far as I am able to determine from figures given of the parts and from a study of the adult animal, Wood-Mason is as likely to be correct as the upholders of the other view. What is badly needed is a study of the ontogeny of the animal.

The homologies of the ventral sacs and of the ventral appendages have been well pointed out by Haase, and seem, like the genital organs, to place the animal somewhere between Diplopoda and Thysanura.

With regard to *Peripatus* it may be said that it possesses such peculiarities of structure that it cannot justly be brought within the group Arthropoda, nor can it be placed with any other group. The most that can be said is that possibly it may be considered as near the ancestral form of annelids, arthropods, and possibly of molluscs, or rather, that it forms an independent branch from this common ancestral form. A similar suggestion was made by Oudemans ('85), who says: "Die Embryologie des *Peripatus* wenigstens meist auf noch frühere, jetzt vielleicht nicht mehr existirende Formen, welche neben den Nemertea oder sogar neben den Cœlenterata zu suchen sind."

The table here given will indicate more clearly than words the similarities and differences in the segmentation and in the position of the genital apertures in the various groups. The asterisks indicate the number and position of the apertures. The brackets indicate fused somites, the ———, a lack of appendages in the adult.

When this paper was partly in type, Schmidt's final article ('95) was received, and hence it could not be used in comparisons. I may state, that it differs in several points from his preliminary account, and in most of these features the results are more in accordance with the account given above.

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Somite	Peripatus	Chilopoda (*Lithobius*)	Hexapoda	Diplopoda	Symphyla	Arachnida (Tetrapneumones)	Xiphosura	Crustacea (Decapoda)
I	Antennæ	———	———	———	———	———	———	———
II	Mandibles	Antennæ	Antennæ	Antennæ	Antennæ	———	———	———
III	Oral papillæ	———	———	———	———	———	———	1st Antennæ
IV	1st legs.	Mandibles	Mandibles	Mandibles	Mandibles	Cheliceræ	1st legs.	2d Antennæ
V	2nd "	1st Maxillæ	Maxillæ	Maxillæ	Maxillæ	Pedipalpi	2d "	Mandibles
VI	3d "	2nd "	Labium	Labial plate	1st legs.	1st legs.	3d "	1st Maxillæ
VII	4th "	Maxillipedes	1st legs.	1st legs. (none in Polydesmidæ)	2d "	2d "	4th "	2d "
VIII	5th "	1st legs.	2d "	2d (or 1st) legs.	3d "	3d "	5th "	1st Maxillipedes
IX	6th "	2d "	3d "	3d (or 2d) " **	4th " *	4th "	6th "	2d "
X	7th "	3d "	———	4th (or 3d) "	5th "	———*	Operculum **	3d "
XI	8th "	4th "	———	5th (or 4th) "	6th "	Lung books	1 gill books	1st Thoracic app.
XII	9th "	5th "	———	6th (or 5th) "	7th "	" "	2d " "	2d " "
XIII	10th "	6th "	———	7th (or 6th) "	8th "	———	3d " "	3d " " ** ♂
XIV	11th "	7th "	———	8th (or 7th) "	9th "	———	4th " "	4th " "
XV	12th "	8th "	———	9th (or 8th) "	10th "	Spinningmammæ	5th " "	5th " " ** ♀
XVI	13th "	9th "	——— ♀*	10th (or 9th) "	11th "	———	Anal segment	1st Abdom. app.
XVII	14th "	10th "	1st Gonapophyses	11th (or 10th) "	12th "	———		2d " "
XVIII	15th "	11th "	——— ♂*	12th (or 11th) "	Stylets	———		3d " "
XIX	16th "	12th "	2d Gonapophyses	13th (or 12th) "	Anal segment	———		4th " "
XX	17th "	13th "	Anal segment	14th (or 13th) "		Anal segment		5th " "
XXI	18th "	14th "		15th (or 14th) "				6th " "
XXII	19th "	15th "		16th (or 15th) "				Anal segment
XXIII	20th "	———*		17th (or 16th) "				
XXIV	21st " *	Anal segment		18th (or 17th) "				
XXV	Anal segment			19th (or 18th) "				
				20th (or 19th) "				

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EXPLANATION OF PLATES.

PLATE I.

Figs. 1-7. *Eurypauropus spinosus* Ryder.
Fig. 1. Female, × about 60.
Fig. 2. Lubbock's supposed eye.
Fig. 3. Penultimate leg, × 160.
Fig. 4. First leg, × 160.
Fig. 5. Antenna.
Fig. 6. Mandible and pharyngeal frame work.
Fig. 7. Newly-hatched young (after Ryder.)
Figs. 8-12. *Eurypauropus ornatus* (From Latzel.)
Fig. 9. Mouthparts; *md*, mandible.
Fig. 10. Mandible more enlarged.
Fig. 11. Antenna.
Fig. 12. Penes.
Figs. 13-18. *Pauropus huxleyi* Lubbock.
Fig. 14. Young as it escapes from the egg (from Lubbock.)
Fig. 15. First leg, × 160.
Fig. 16. Anal leg, × 160.
Fig. 17. Penultimate leg, × 160.
Fig. 17^{b}. Foot of same, × 600.
Fig. 18. Antenna of *Pauropus pedunculatus* Lub.
Fig. 19. Penes of *Polyxenus lagurus* (from Latzel.)

PLATE II.

Fig. 21. The antenna and antennal tip of *Lysiopetalum lactarium* showing the terminal jointed sensory hairs, ×$\frac{1}{1}$20.

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Fig. 22. The globulus of *Pauropus huxleyi*, × 1300.
Fig. 23. Antenna of same, × 590.
Fig. 24. Tip of the flagellum of same, × 1300.
Fig. 25. Tip of stylus latior, globulus and bases of the flagella of *Eurypauropus spinosus*, × 1300.
Fig. 26. Two annuli of a flagellum with an included air bubble.
Fig. 27. End of flagellum of *E. spinosus* with two air bubbles.
Fig. 28. Tip of antenna of larva of *Toxotus curso*, showing the "appendix sessilis articuli secundi" (*a*) (after Schiödte.)
Fig. 29. Same in *Cyrtomerus pillicornis* (after Schiödte.)
Fig. 30. Same in *Clytus mysticus* (after Schiödte.)
Fig. 31. Same in *Saperda carcharias* (after Schiödte.)
Fig. 32. Same in an American beetle larva.
Fig. 33. "Stipes palpi maxillaris cum mala exteriore palpoque" of the larva of *Pogonochoerus pilosus* (after Schiödte.)
Fig. 34. Optical section of the globulus of *E. spinosus*. *gl*, bulb; *h*, hair; *st*. stalk.
Fig. 35. Hairs of third and fourth antennal joint of *P. huxleyi*.
Fig. 36. Section of stylus angustior in *E. spinosus* showing terminal sensory ganglion, × 625.
Fig. 37. Section of stylus latior in same antenna.
Fig. 38. Clavate hair of head of *P. huxleyi*.
Fig. 39. Branched coxal hair from anal leg of same.
Fig. 40. Coxal hair of *E. spinosus*.
Fig. 41. Ventral hairs of *Polyxenus*.
Fig. 42. Caudal styliform hairs of *Pauropus huxleyi*, × 600.
Fig. 43. Sensory ganglion of a lateral tactile hair of *E. spinosus*, × 600.
Fig. 44. One of fourth pair of tactile hairs of same.
Fig. 45. Cross section of a dorsal plate of *E. spinosus* near the hinder edge where it forms a fold before its union with next plate. The lower spiny surface is therefore morphologically the upper surface. One chitinous pillar connects the two cuticular layers thus produced and cuts off a small mass of hypodermal cells together with a nucleus of a fat-body cell.

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Fig. 46. Same farther back showing more pillars and smaller cell-masses.

Fig. 47. Longitudinal section of the cuticle of a dorsal plate of *E. spinosus*.

Fig. 48. Surface of dorsal plate with hooked spines and wart-like protuberances.

Fig. 49. Hypodermal cells and fat-body cells of *E. spinosus*.

Fig. 50. Fat-body cells with large nuelei.

PLATE III.

Fig. 50 bis. Wall of mid-gut of *Pauropus huxleyi* with crystals removed, showing vacuolated character of cytoplasm, × 600.

Fig. 51. Crystals from lumen of mid-gut of *E. spinosus*, × 1300.

Fig. 52. Junction of fore and mid guts in same.

Fig. 53. Section through anterior constricted portion of hind gut of same, showing outer layer of cells more prominent than usual, × 600.

Fig. 54. Junction of mid and hind gut; the former at the left, × 600.

Fig. 55. Near junction of constricted part of hind gut with rectum in *P. huxleyi*, the small piece of the latter showing the two muscular layers, × 300.

Fig. 56. Transverse section of rectum of *P. huxleyi*, showing a bit of the anterior part of hind gut at one side.

Fig. 57. Transverse section of salivary gland of *E. spinosus*.

Fig. 58. Fat-body and vacuolated anterior Malpighian tube of *E. spinosus*.

Fig. 59. Origin of a Malpighian tube in *E. spinosus*, × 600.

Fig. 60. Similar section, the cells containing crystals.

Fig. 61. Same, a little anterior.

Fig. 62. Section near the end of mid-gut of *P. huxleyi* ♂ showing groups of cells simulating sections of Malpighian tubes.

Fig. 63. Middle portion of Malpighian tube from same individual as fig. 59.

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Fig. 64. Nearly sagittal section through head region of *E. spinosus*. *coc*, œsophageal commissure; *f. l*, frontal lobe; *ant. n*, antennal nerve.

Fig. 65. Section through brain, œsophageal commissure and first ventral ganglion of *P. huxleyi*, × 300.

Fig. 66. Section of brain of *E. spinosus*. *p. l*, posterior lobe; *ant. l.* antennal lobe; *fg*, foregut with two muscle bands below.

Fig. 67. Anterior part of glandular portion of oviduct of *E. spinosus*. *ovd*, oviduct; *rs.*, receptaculum seminis.

Fig. 68. Junction of oviduct, and duct of receptaculum seminis of *E. spinosus* at the genital opening, to the right of the median line.

Fig. 69. Posterior end of glandular oviduct of same. A few large crystals are shown in the intestine above.

Fig. 70. More posterior section showing the most mature ova.

PLATE IV.

Fig. 71, 72. Reconstructions of the male genital system of *P. huxleyi*. *dea*, ductus ejaculatorius anterior; *gla*, glandula accessoria; *depd*, duct. ejac. post. dexter; *j*, vesicular tube not connected with the rest of the system; t^1, t^2, anterior and posterior testicular masses; *ves*, vesiculæ seminales; vd^{1-3} vasa deferentia; *y*, union of vesicular tubes; 1-4 loops, processes and anastomoses.

Fig. 73. Section of glandular part of ductus ejaculatorius.

Fig. 74. Section of duct. ejac. post. communis.

Fig. 75, 76, 77. Section of vesiculæ seminales.

Fig. 78. Section of unconnected portion, *j* in fig. 72.

Fig. 79. Testis with indications of the mode of spermatogenesis.

Fig. 80. Vas deferens.

Fig. 81. Reconstruction of brain and anterior ventral ganglia of *E. spinosus*, from above.

Fig. 82. Brain of Eurypauropus from in front.

Fig. 83. Same in sagittal section with ventral cord and intestine. This and fig. 82 from reconstructions. *ant.*

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n, anternal nerve ; *cf*, central foramen ; *co*, œsophageal commissures ; *fg*, frontal ganglion ; *f l*, frontal lobe; g^1-g^4, ganglia of ventral cord ; *mg*, mid-gut, *seg*, subœsophageal ganglion.

Fig. 84. Reconstruction of ovary. *rs*., receptaculum seminis ; *oda* and *odp*, anterior and posterior oviduct.

Fig. 85. Reconstruction of alimentary tract. *fg*, fore-gut; *hg*, hind-gut; *mg*, mid-gut; *mpg*, Malpighian tubes ; *rect*, rectum ; *sgl*, salivary gland.

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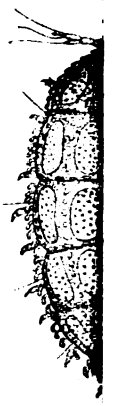

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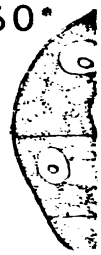

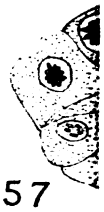

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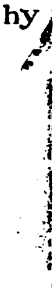

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TUFTS COLLEGE STUDIES, No. 5.

THE CHONDROCRANIUM IN THE ICHTHYOPSIDA.

GUY M. WINSLOW.

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TUFTS COLLEGE STUDIES, NO. 5.

THE CHONDROCRANIUM IN THE ICHTHYOPSIDA.[1]

By Guy Monroe Winslow.

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[1] Studies from the Biological Laboratory of Tufts College, under the direction of J. S. Kingsley, No. XIX. Reprinted from the Bulletin of the Essex Institute, Vol. XXVIII, pp. 87-141.

I wish here to give credit for some of the material used in these studies. The Necturus larvæ were given to me by Miss Julia B. Platt; for Pipa I am indebted to the late Professor E. D. Cope; Professor Robert Wiedersheim furnished me with the Protopterus material and I began the study of the chondrocranium of this Dipnoan in his laboratory. For Amphiuma I am indebted to Professor O. P. Hay, the first to find embryos of this interesting Urodele, and to the late Professor John A. Ryder, who kindly turned over to me the embryos sent him by Doctor Souchon of New Orleans. The embryo Cæcilians were given me by the cousins Paul and Fritz Sarasin and were a part of the material which formed the basis of their splendid monograph. To all these I return my best thanks.

J. S. Kingsley.

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INTRODUCTION.

THE work, the results of which are given in the following pages, has been carried on in the Biological Laboratory of Tufts College, under the direction of Dr. J. S. Kingsley, to whom the author is deeply indebted, not only for the use of much of the material studied, a considerable part of which was already prepared, but far more for invaluable aid and encouragement during the preparation of this paper. It is also due to Dr. Kingsley to acknowledge the free access to his private library containing a large portion of the literature upon the subject, and to state that the models of the first stage of Amphiuma and the three stages of Necturus were made by him.

In my account of the development of the chondrocranium I have not attempted to treat of the origin of the pro-cartilage cells, but I begin with the first formation of cartilage. These earlier stages have been so ably described by Miss Platt ('93, '94) that there seems no necessity to repeat her account, especially as her discoveries in regard to the ectodermal origin of the cartilage-forming cells were largely made in this laboratory, and have received general support and confirmation in the papers of Kastschenko ('88), Goronowitsch ('92, '93, '93[a]), Klaatsch ('94, '95) and von Kupffer ('95).

One object in these investigations was to ascertain to what extent the primary cranial structures throw light upon some problems in the classification of certain Ichthyopsida. The principal of these problems were these:

(1) By most students the Cæcilians have been recognized as a distinct order of Batrachia, but more recently the late Professor Cope in several papers has maintained that these forms were in reality aberrant Urodeles and

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should have only family rank in that order. Summarizing his conclusions, he maintained that the Cæcilians were descended from Amphiuma-like forms and these in turn were offshoots from some amblystomoid Urodele. The cousins Sarasin, while agreeing with Professor Cope in the view that the Cæcilians and Amphiuma were nearly related, regarded the relationship as differing in this respect. Amphiuma was a neotenic Cæcilian, a larval Cæcilian become sexually mature. My problem was to ascertain in how far the chondrocranial structures gave support to any of these views.

(2) The fact that the Dipnoi possess lungs led to the view, which has obtained wide acceptance, that these ancient fish-like forms were the ancestors of the Batrachia, and this view has received no little support from Huxley's short but most suggestive discussion of the suspensorial apparatus in the Ichthyopsida. More recently several students have maintained that the Batrachia have sprung from the Crossopterygian Ganoids and that the only relationship that can be traced between Dipnoi and Amphibians is that the lung-fishes may have had the same ancestry, but that they can in no wise be considered as in the line of batrachian descent. In how far does the chondrocranium support either of these views?

It has not been my purpose to enter the broader field of the relationships of these different groups as is shown by other features. I have confined myself closely to the chondrocranium and my results are to be regarded as merely one factor in deciding these questions; a factor in itself of minor importance.

I take as the basis of my studies the development of the chondrocranium of *Amblystoma punctata*, since of this form I have had the most abundant material. This is followed by an account of certain stages of the chondro-

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crania of some other Ichthyopsida, and an attempt is made to see how far the chondrocranium can be employed as an aid in the classification of these forms.

The various stages are determined in an arbitrary manner by body length, but it is to be borne in mind that there is considerable variation in embryos and larvæ of the same size. All stages described have been modelled in wax by Born's method, the models have afterwards been carefully measured and compared and all exaggerations of proportion due to slight variations in the thickness of the wax have been corrected in the drawings.

AMBLYSTOMA PUNCTATA.

FIRST STAGE. *Embryo ten mm. long. Mouth on the point of breaking through* (Figs. 1 and 2).—This stage, which I have taken as the starting point of my investigations, corresponds closely with that at which Ph. Stöhr begins his classic account of the chondrocrania of Triton and the Axolotl ('79). The chondrocranial elements are still in the pro-cartilage condition but they are clearly differentiated from the surrounding parts by the arrangement of their cells. Three pairs of elements are present, namely, the parachordals, trabeculæ and the quadrates.

The parachordals (*p*) lie as two triangular plates upon each side of the slightly depressed anterior end of the notochord. One side of each triangular plate is directed anteriorly and the antero-exterior angle joins the posterior end of the trabecula, while the inner face of each abuts against the side of the notochord (*n*). The lateral margin of the parachordal runs obliquely outwards and forwards from its posterior angle to the junction with the trabecula. The parachordals arise separately and at this stage touch only at the sides of the notochord, thus leav-

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ing the upper and under surfaces and the tip of the latter exposed.

The trabeculæ (*t*) continue forwards in nearly the same horizontal plane as the main part of the notochord, the apex of which, with the adjoining portions of the parachordals, is slightly depressed. The trabeculæ curve first outwards to a point beyond their middle and then in, their apices being about as far apart as their bases. They end medially to the olfactory organs, a little behind the external narial openings. The lower margin of each trabecula is thickened, while above it is developed into a high and thinner crest (*trc*) inclining slightly outwards. The upper margin of this crest is extremely irregular and the foramina for the optic and oculomotor nerves (*of* and *oc*) are but partially enclosed. The crest gradually increases in height from in front backwards to the posterior end of the trabecula where it terminates abruptly.

The quadrates appear as two thin bands of cartilage external to and at some distance from the parachordals. They are concave anteriorly and their general direction is downwards and outwards. In each quadrate can be already recognized three portions, a middle piece constituting a body (*bq*) from which arise an upper ascending process (*ap*) directed forward, inward and upward toward the crest of the trabecula, and a lower descending process (*dp*) running outward, forward and downward to the articulation with Meckel's cartilage. The body is somewhat lenticular while the processes are thin and more laminate.

Meckel's cartilage (*m*) is already complete. The general course of each ramus is obliquely inward and forward until about the middle point where it curves still more strongly inward to meet its fellow of the opposite side. At its base each ramus is stout but it tapers regu-

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larly and is slender at the point of union. A point which seems to me of considerable morphological importance is that the symphysis is considerably behind the apices of the trabeculæ, recalling in this embryonic stage the conditions which are permanent in the Elasmobranchs and lower Ganoids.

SECOND STAGE. *Embryo, eleven mm. long* (Fig. 3).—The parts described in the first stage have chondrified rapidly and two new pairs of cranial elements, the otic capsules and the two processes of the occipital arch, have made their appearance.

The occipital arch (*ocp*) is composed of two isolated conical pieces of cartilage, the bases of which rest upon the sides of the notochord a little behind the otic region. From the notochord they curve outwards and upwards, half encircling the medulla and terminating freely. The incompletely developed otic capsules (*o*) are represented by thin layers of cartilage, very irregular in outline, covering the lateral and portions of the dorsal and ventral surfaces of the auditory vesicles. Their anterior ends lie immediately behind and above the bodies of the quadrates while their posterior ends are somewhat nearer the median line, just in front of the occipital arch. The ventral walls of the two capsules are in nearly the same horizontal plane with the notochord and the parachordals. There are no cartilaginous connections between the capsules and the rest of the chondrocranium.

The parachordals (*p*) have fused with each other at the apex of the notochord and now extend back along its sides to about the middle of the otic region where each gives off a lateral process which underlies the median portion of the sacculus. Although the median wall of the otic capsule is as yet but slightly developed, its future line of fusion with the parachordal is clearly indicated by a longitudinal marginal thickening of the latter.

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Accompanying the general growth of the head and the lessening of the cranial flexure, the trabeculæ (*t*) have increased considerably in size, more especially in length. At their anterior ends they have become slightly broadened and flattened to form the cornua trabeculæ (*c*), the first indications of the nasal capsules. The gaps between the disconnected portions of the trabecular crest of the first stage are now filled, forming a plate, the dorsal margin of which is a smooth, undulating line sloping gradually downward in passing from behind forwards. The foramina for the optic and oculomotor nerves are now completely enclosed.

Several noteworthy changes have occurred in the quadrate (*q*). Its body and descending process have grown broader and thicker, and two lateral projections from the latter form a transitory support at the base of the balancer (*su*). At the time of its most complete development this support has the form of a shallow cup, the rim of which coincides with the circumference of the base of the balancer. The ascending process has extended upward and has fused with the posterior end of the trabecular crest. A slight backward projection from the body of the quadrate is the first trace of the otic process.

THIRD STAGE. *Larva twelve mm. long* (Figs. 4–7).—The distal ends of the occipital processes (*ocp*) have fused with the postero-dorsal walls of the otic capsules, and their proximal ends have fused with the posterior ends of the parachordals. A solid floor is thus formed beneath the medulla, and the jugular foramen (*j*) is enclosed by cartilaginous walls.

The parachordals (*p*) with the notochord now form a complete basilar plate below the posterior half of the brain cavity except at one small place (*f*) upon the left side which still remains unchondrified. With the excep-

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tion just mentioned, the lateral margins of the parachordals are now everywhere continuous with the floors of the otic capsules.

The otic capsule (*o*) now presents the typical capsular form, covering by far the greater part of the surface of the auditory vesicle. The median wall is beginning to form along the dorsal margin and at the two ends of the capsule, leaving two unchondrified spaces in the middle and ventral region; a large anterior one through which pass the seventh and eighth nerves and the endo- and perilymphatic ducts, and a smaller fontanelle lying postero-dorsally to the first. In the floors of the capsules are the foramina for the exit of the branches of the seventh nerve (*vii*). Upon the left side the two branches of this nerve pass through the two ends of a transversely elongated foramen, while upon the right side they pass through two separate foramina formed by the fusion of the middle portions of the anterior and posterior walls of the originally elongated foramen. Behind the foramina for the seventh nerve and somewhat farther laterally is the large fenestra ovalis (*fo*). The stapes (*s*) which arises from a separate centre of chondrification occupies the anterior end of the fenestra.

The only noteworthy changes in the trabeculæ are a general strengthening and an increase in the size of the cornua (*c*). The quadrate has become more solid throughout all its parts except the processes which were at the base of the balancer in the preceding stage. They have disappeared together with the balancer, leaving a single conical process in the place they formerly occupied. The otic process (*op*) extends considerably farther backwards than before.

FOURTH STAGE. *Larva thirty-nine mm. long. Gills not yet atrophied* (Figs. 8–11).—The ventral portion of

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the occipital arch is in essentially the same condition that it was in the third stage. So also are the parachordals, except that the union with the capsular floor is now complete upon both sides.

The otic capsules present several new features. From their point of fusion with the occipital processes marginal expansions (Figs. 9 and 11, *loc*) extend medially over the sides of the cranial cavity. Passing forwards they approach each other and unite to form the synotic tectum (*st*) which terminates anteriorly in a short median process (*tm*) the "tænia tecti medialis" of Gaupp. In the median wall of the capsule there are now four small apertures, of which three (Fig. 11) lie in a horizontal row near the floor of the cranium, while the fourth is more dorsal in position. Passing from in front backwards, the first foramen of the row is the one traversed by the seventh and one branch of the eighth nerve (*vii*+*viii*). The second branch of the eighth passes through the second foramen (*viii*), and the third aperture of the row is traversed by the perilymphatic duct (*pf*). The fourth aperture, higher up in the wall above the foramen for the second branch of the eighth nerve, is the foramen for the endolymphatic duct (*ef*).

At the anterior end of the otic capsule there are three new connecting cartilages joining it with the trabecula on the one hand, and on the other with the quadrate. The process joining the postero-dorsal point of the trabecular crest with the opposite wall of the capsule is relatively slender; while the other two processes, the otic (*op*) and palato-basal (*pb*), are formed by the fusion of a greater part of the dorso-median surface of the body and otic process of the quadrate with the adjacent wall of the capsule and the margin of the basilar plate. A blood vessel, which passes dorso-ventrally around the anterior end of

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the capsule, is the only line of demarcation between the otic and palato-basal processes. A large chamber is enclosed between the posterior end of the trabecula, the anterior end of the capsule and the bars connecting them dorsally and ventrally. The ascending process of the quadrate passes across its external surface, separating a dorsal and a ventral foramen. The Gasserian ganglion occupies this chamber and from it pass out the ramus ophthalmicus profundus (*rp*) through the ventral foramen, and the rami ophthalmicus superficialis (*rs*), maxillaris (*rm*), and mandibularis (*rn*), through the dorsal foramen.

The foramina by which the rami of the seventh nerve leave the otic capsule are unchanged, except that now there are two upon each side and that they are considerably reduced in size. The fenestra ovalis (*fo*) is now nearly filled by the stapes (*s*), which has a slight prominence directed outwards and upwards from the antero-dorsal angle of the cartilage towards the otic process of the quadrate. These cartilages, however, do not become united at any time during the development of Amblystoma as they do in some other forms.

The trabeculæ (*t*) are of nearly uniform size from their junction with the parachordals to the point where they meet in front in the ethmoid plate (*e*). Optic and oculomotor foramina are of equal size, both being small. The ethmoid plate (*e*), arising by the fusion of the anterior ends of the trabeculæ in the median line, forms a continuous floor beneath the anterior end of the cranial cavity, the nasal septum (*ns*) and portions of the olfactory organ. In front it terminates upon each side in a conical process. Laterally a freely ending process (*c*) extends backwards along the ventral surface of the olfactory organ. This and the adjacent parts of the ethmoid plate are develop-

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ments of the cornua of the earlier stages. In the same plane with the ethmoid plate and just behind its posterior end, a flat antorbital process (*anp*) projects from the side of the trabecula and, curving forwards, terminates directly behind the backward projecting process of the ethmoid plate.

A broad nasal septum rises from the middle of the ethmoid plate separating the two olfactory organs and forming the anterior wall of the cranial cavity. Bars of cartilage, which I have called the tectal cartilages (*tc*), connect the antero-dorsal points of the trabeculæ with the opposite points of the septum, roofing over the olfactory foramina and forming the bases from which curved processes, laminæ cribrosæ (*e*), extend outward, downward and forward, covering over the posterior ends of the olfactory organ.

The quadrate (*q*), besides its fusion with the otic capsule as already mentioned, now presents a well developed pterygoid process (*pt*), a cylindrical rod of cartilage joining the main part of the quadrate at the point where the ascending process meets the body. Its general direction is forwards, parallel with the trabecula as seen from above, and downwards with a slight outward curve near the tip which lies just below the ventro-median surface of the orbit.

FIFTH STAGE. *Young Amblystoma sixty-nine mm. long. Gills entirely atrophied* (Figs. 12–13).—At this advanced stage in the development of Amblystoma, ossification has occurred to so great an extent that large portions of the older cartilages have disappeared, giving the chondrocranium a broken and ragged appearance, especially in the otic region. The median capsular wall, the anterior end of the basilar plate and portions of the occipital arch, and the trabeculæ are entirely replaced

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by bone. At the same time the whole skull has increased in breadth as compared to its length.

The synotic tectum (Fig. 12, *st*) is completely separated from the remnants of cartilage forming the otic capsules, and the basilar plate (*p*) is reduced in length to little more than that of the tectum. Ossification has removed nearly all of the cartilage of the capsule behind the posterior end of the fenestra ovalis where the stapes is now closely applied against the remnant of the cartilaginous wall of the capsule.

The quadrate (*q*) has undergone important changes, due in part to ossification and to the lateral expansion of the skull. Its body is thicker antero-posteriorly and stands out farther from the capsule. The descending process is cylindrical in shape, presenting greater definiteness of outline than previously. Irregular perforations of the cartilage occur along the line where the quadrate joins the capsule. Most striking of all is the change in the position of the pterygoid process (*pt*) which, instead of being nearly parallel with the long axis of the skull as in the previous stage, now slants from its base outwards at an angle of about thirty degrees from that axis.

The cartilaginous nasal capsules have reached their highest stage of development and present many new and important features. The nasal septum (Fig. 12, *ns*) is narrowed down to about half its former width. In front it divides into two doubly curved plates which extend forwards and outwards to the cup-like anterior ends of the capsules. From the ventro-median surface of each of these plates a short knob-like process extends forwards and terminates the capsule anteriorly.

A flattened band of cartilage which I have called the ventral process (*vp*), in contradistinction to the dorsal

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process (*d*) to be described later, passes backwards from the ventral margin of the cup-like anterior end of the capsule. At its posterior end this process fuses laterally with the lamina cribrosa (*l*) while medially it terminates in a process projecting freely backward (Fig. 13, *vp*).

The cylindrical dorsal process (*d*) extends diagonally across the anterior end of the olfactory organ from the dorso-median margin of the cup to the anterior end of the lamina cribrosa. A short connecting rod joins the dorsal process and lamina cribrosa with the ventral process in front of the nasal duct (*nl*). As in the preceding stage, the lamina cribrosa forms a roof over the posterior end of the olfactory organ. It now reaches downwards to meet the outer end of the antorbital process thus enclosing the orbito-nasal foramen (*on*), and outwards and forwards to meet the ventral and dorsal processes as described above. It is perforated near the lateral margin by several small foramina through which pass a branch of the ophthalmicus profundus (*rp*) and some small blood vessels (*b*). A branch of the nasalis internus (*ni*) passes out of the capsule through the foramen in its median wall.

DESMOGNATHUS FUSCA (Fig. 14).

The chondrocranium of *Desmognathus fusca*, of which I have modelled two stages, presents so great a similarity to the earlier stages in Amblystoma that only a few words need be devoted to it. Figure 14 represents the model of the skull of an embryo about twenty mm. long.

The parachordals (*p*) are represented by three narrow bands of cartilage; one extending between the posterior ends of the otic capsules and having the notochord partly imbedded in it, and two other bands which connect the apex of the notochord with the posterior ends of the trabeculæ.

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The entire absence of a stapes in the history of the chondrocranium is the only noteworthy point of difference between the formation of the ear capsules in Desmognathus and in Amblystoma. The trabeculæ and quadrates present conditions essentially the same as those of a corresponding stage in Amblystoma, but owing, in part at least, to the early appearance of the bony skull in Desmognathus no complex nasal capsule is formed. The simple condition shown in Fig. 14 is the highest state of development reached by the anterior ends of the trabeculæ. A small antorbital process develops in the usual place upon the side of the trabecula. No pterygoid process of the quadrate appears in either of the stages modelled. As the older stage presents a state of development approximately equivalent to that found in the fifth stage of Amblystoma the appearance of this process as figured by Wiedersheim ('77) must be a comparatively very late occurrence.

PLETHODON GLUTINOSUM (Fig. 15).

From a specimen of *Plethodon glutinosum* twenty mm. in length and showing the chondrocranium in an advanced stage of development, I have modelled the nasal capsules. In regard to the rest of the skull mention of a few points will suffice.

In the main it corresponds closely with the skull of Amblystoma as described in our fifth stage (Figs. 12 and 13). This similarity is especially noticeable in the position of the pterygoid process. There is a stapes, the antero-dorsal point of which, unlike that of Amblystoma, is connected to the quadrate by a very slender stapedial process. The otic and palato-basal processes present the usual conditions.

Aside from the rod connecting the dorsal and ventral

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processes in front of the narial duct all the parts described for the nasal capsule of Amblystoma are found in approximately the same positions in Plethodon with unimportant modifications as to relative sizes. This similarity is even more apparent in older specimens of Plethodon than in the one from which this model was made. The two small foramina in the lamina cribrosa mark the points at which a branch of the ophthalmicus profundus (*rp*) enters and leaves the capsule.

NECTURUS MACULATUS.

Cope ('89) has placed *Necturus maculatus* with its American relative *Necturus punctata* and the European Proteus in a group together under the name Proteida with the remark that they occupy a position intermediate between the Stegocephali and the Urodela, and differ from the latter mainly in the possession of an intercalary bone. Descriptions of three stages in the development of the chondrocranium of *Necturus maculatus* are here given.

FIRST STAGE. — The first stage represents the skull of an embryo twenty-one mm. in length, and corresponds approximately to the condition found in Amblystoma at a time a little earlier than that represented in the third stage of the latter (Figs. 4-7). The occipital arch consists of two processes extending upward from the sides of the notochord and ending freely above. At their bases they are connected with the posterior ends of the parachordals.

The parachordals run forward from the bases of the occipital processes, slightly removed from the sides of the notochord. Between the posterior ends of the otic capsules they bend inwards and touch the sides of the notochord to which they are attached for a short distance, then curve sharply outward, and, fusing laterally with the cap-

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sular floors, continue forward into the trabeculæ. The notochord projects forward some distance in front of the most anterior point at which the parachordals touch its sides. The otic capsules are widely separated and incompletely formed. Their floors are partially attached to the parachordals and the only traces of the median wall are found around the inner margins of its walls. A large fenestra ovalis, with no stapes, and a large foramen for the exit of branches of the seventh nerve constitute the only well defined apertures which are found in later stages.

The trabeculæ extend forwards from the anterior ends of the parachordals as long slender rods running parallel for the posterior three-fourths of their length and then bending inward at an angle of about thirty degrees towards the median line, which they do not reach. There are, as yet, no foramina for the second and third nerves and only a slight trace of a trabecular crest to which the ascending process of the quadrate is attached.

The quadrate is wedge-shaped as seen either from the side or in front, the point being directed ventrally. A short otic process extends upward and backward from the dorso-lateral angle of the wedge and fuses with the otic capsule, while a longer ascending process extends upward and forward from the dorso-median angle and fuses with the dorsal end of the slightly developed trabecular crest.

SECOND STAGE. — Our second model is that of an embryo twenty-four mm. in length. The occipital processes are fused distally with the walls of the otic capsules and continue along the dorso-median angles of the capsules as the beginnings of the synotic tectum. The jugular foramen is at this stage a dorso-ventrally elongated slit.

In place of the distinctly outlined parachordals of the previous stage we now have a continuous basilar plate

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lying beneath that portion of the cranial cavity included between the posterior halves of the otic capsules. As before, the notochord projects freely forward in the median line. Laterally and in front the basilar plate merges into the capsular floors and the trabeculæ.

The otic capsules present essentially the same conditions found in stage three of Amblystoma (Figs. 4–7) except that the otic process of the quadrate is fused with the antero-ventral surface of the capsule. A trabecular crest just large enough to enclose the optic and oculomotor foramina and to form a point of attachment for the ascending process is now developed. The appearance of simple antorbital processes upon the sides of the trabeculæ is the only further change which needs mention here.

THIRD STAGE. *Larva forty-five mm. long* (Fig. 16). — A continued fusion of the margin of the occipital process with the wall of the otic capsule, resulting in a reduction of the size of the jugular foramen, is the most noticeable change in this region. The synotic tectum is now fully developed and presents the usual form. The basilar plate remains the same as in the previous stage.

The otic capsules have reached their highest state of development. The median wall is perforated by four foramina which correspond almost exactly to those described for the otic capsule of the fourth stage of Amblystoma (Fig. 11). In fact the only differences of any importance between the otic regions of this skull and that described as the fourth stage for Amblystoma are in the absence of the parachordals at the anterior end of the notochord, and the more median position of the foramen for the palatine nerve (*pal*). A small crest is now developed along the posterior half of the trabecula. A slender connecting rod unites the posterior end of the crest with the opposite wall of the otic capsule. Antorbital processes project outward and forward from the sides of the trabeculæ.

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By a fusion of the anterior ends of the trabeculæ in the median lines a small ethmoid plate is formed, upon the anterior end of which is a slight prominence, the only indication we have of a nasal septum. Upon each side a short forward-projecting process terminates the ethmoid plate anteriorly.

Entirely separated from the rest of the cartilaginous parts of the head there is now a delicate nasal capsule (Fig. 16, *nc*). It consists of a curved rod, which runs along the dorso-median surface of the olfactory organ, following more or less closely the direction of the anterior end of the trabecula and the ethmoid plate, and a number of shorter processes projecting laterally from this main rod over the top of the olfactory organ. As Pinkus ('94) has pointed out, there is some resemblance between this nasal capsule and that of Protopterus, but it seems to me hardly necessary, for reasons which will appear more fully later, to attach any importance to this similarity other than that of a coincidence.

One would seem justified in expecting that, if Necturus occupy a position intermediate between the Stegocephali and the Urodela, the chondrocranium of Necturus would show more or greater differences from the typical Urodele chondrocranium than are found in higher Urodeles, the Urodela of Cope. But I am unable to discover that this is the case. It would be difficult, rather, to point out a form in which the chondrocranium is more typically Urodelan.

AMPHIUMA MEANS.

The first of the two models of the chondrocranium of *Amphiuma means* here described is the one which formed the basis of the description of the chondrocranium in Dr. Kingsley's preliminary paper upon "The Head of an Embryo Amphiuma" ('92). The chondrocranium of

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another specimen from the same lot of embryos was also described and figured by Professor O. P. Hay in his paper of '90.

FIRST STAGE (Figs. 17–18).—The occipital processes have fused with the otic capsules and their distal ends project inward over the sides of the cranial cavity as the first steps in the formation of the synotic tectum. The parachordals (Fig. 18, *p*) extend forward from the bases of the occipital processes, and, after curving inward to the sides of the notochord and fusing beneath it, they each divide into a median and a lateral band. The lateral bands of the two sides curve outward and, fusing with the capsular floors, pass forward to the posterior ends of the trabeculæ. The median bands separate in front of the apex of the notochord, bend laterally and join the lateral bands again at their junction with the trabeculæ. Between these two parts of each parachordal a fontanelle is enclosed.

The otic capsules present nearly the same condition as that found in the fourth stage of the skull of Amblystoma. But here, as was also noted in Necturus, the foramen for the palatine branch of the seventh nerve (*pal*) is on the median side of the median capsular wall.

The trabeculæ extend from their union with the parachordals forward to the nasal region, where they fuse in a small ethmoid plate which is terminated anteriorly by two broad triangular cornua. Along the middle and posterior end of each trabecula is a well-developed crest covering in the optic and oculomotor foramina as usual. It is connected postero-dorsally with the anterior end of the otic capsule, and it is also connected with the median angle of the quadrate by means of the ascending process (*ap*). The point at which the ascending process joins the trabecula is relatively farther anterior in Amphiuma than in Amblystoma, thus producing more elongate foramina for the exit

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of the nerves coming from the Gasserian ganglion (Fig. 18, *v*). Antero-dorsally the crest gives rise to a rod of irregular shape, which projects forward, outward and downward. This is the lamina cribrosa (*e*). Below and a little behind this the antorbital process is just beginning to appear upon the side of the trabecula.

The quadrate is rhomboidal in outline when viewed from the side. It is connected with the trabecular crest by the ascending process, as mentioned above, but as yet it has not fused with the otic capsule. From its posterior angle a slender stapedial process (Fig. 17, *sp*) extends backward into the anterior end of the fenestra ovalis where it joins the small stapes. No pterygoid process is yet developed. Meckel's cartilage articulates with the antero-ventral surface of the quadrate.

SECOND STAGE (Fig. 19).—In the second stage of the chondrocranium of Amphiuma, ossification is far advanced. The most important additions to the cartilages are seen in the completed nasal capsule and the pterygoid process (*pt*) of the quadrate which is now developed.

The distal ends of the occipital processes have developed into a narrow synotic tectum, while the notochord and median portions of the parachordals have disappeared except in the occipital region, where they form a ventral band (*p*) connecting the two capsules. No changes worthy of notice have taken place in the otic capsules aside from the results of ossification.

The trabeculæ are divided into anterior and posterior portions by ossification in the orbital region. The posterior portion remains essentially the same as in the first stage, but the anterior portion is changed by the formation of the nasal capsule. The base of the antorbital process (Fig. 19, *anp*) marks the posterior end of that portion of the trabecula remaining unossified in front of

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the optic foramen. A narrow column of the trabecular crest projects upwards from just in front of the base of the antorbital process, and upon the anterior end of the ethmoid plate a thin nasal septum is developed. Two cartilages upon each side arise from the dorsal end of the septum. From its posterior end a cylindrical rod, the tectal cartilage (*te*) extends backward and outward to the dorsal point of the remnant of the trabecular crest. From the posterior end of the septum a band of cartilage extends forward and expands into a broad sheet, the nasal tectum, roofing over the whole anterior portion of the olfactory organ. Where the nasal duct passes out to the exterior (*nl*) at the anterior end of the tectum, a complete ring of cartilage encircles it. Laterally the nasal roof is connected by a band curved ventrally with the cornu (*c*) of the trabecula. And from the postero-lateral margin of the tectum a flattened rod (*l*) passes backward to the tectal cartilage, fusing with it at a point just above the anterior end of the antorbital process.

While it is impossible to homologize all the parts of the nasal capsule of Amphiuma with those in Amblystoma there are some points in which the similarity between them is very close. The septa, ethmoid plates, and tectal cartilages are essentially alike in both. The lamina cribrosa and dorsal process of Amblystoma are represented in Amphiuma by the rod connecting the tectal cartilage with the nasal tectum. The open anterior end of the capsule of Amphiuma is quite different from the cup-like end of Amblystoma to which it must be compared. This difference in the capsules is, of course, correlated with the relative change of position of the nostrils, which are at the anterior end of the capsules in Amphiuma and in the middle of the sides of the capsules in Amblystoma. In Amphi-

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uma the antorbital process does not become fused with the lamina cribrosa.

The quadrate is now supplied with a pterygoid process (*pt*) which runs forward from the ventral surface of the ascending process in close proximity with the ventral margin of the trabecula. Towards its anterior end it curves laterally and broadens out into an oval plate. Its anterior end lies a short distance postero-laterally from the base of the antorbital process. Otic and palato-basal processes unite the quadrate with the otic capsule. The stapes has expanded into a broad plate nearly filling the fenestra ovalis. It is still connected with the quadrate by a strong stapedial process (*sp*).

CHARACTERISTICS OF THE URODELE CHONDROCRANIUM.

From the preceding descriptions of the chondrocrania of various Urodeles, we may briefly enumerate the more important characteristics of the cartilaginous skull as found in this group.

Two occipital processes, the early history and relationships of which have been more fully treated by Ph. Stöhr ('79), arise independently at the sides of the notochord in front of the first permanent vertebra. The similarity between these processes and those of which the vertebræ are formed clearly indicates the vertebral nature and origin of the occipital arch. From the sides of the notochord the occipital processes pass upward, fuse with the walls of the otic capsules and bend over medially to form the synotic tectum (Fig. 18, *ocp*). Two large jugular foramina are enclosed between the bases of the occipital processes and the posterior ends of the otic capsules. Parachordals, varying in size and extent from the narrow bands of Desmognathus (Fig. 14, *p*) to the complete

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basilar plate of Amblystoma (Figs. 9 and 10 *p*), form a more or less complete floor beneath the otic portion of the brain cavity. The otic capsules are approximately oval in shape and in all cases have a median wall distinctly separating the cavity of the capsule from that of the brain. There are generally four foramina in this wall through which pass the seventh and eighth nerves and the endolymphatic and perilymphatic ducts. In the ventro-lateral wall of the capsule there is a large fenestra ovalis which may or may not be occupied by a stapes. When present the stapes appears first at the anterior end of the fenestra and only later, if at all, does it reach back to the posterior wall of this aperture. The stapes may be connected with the quadrate by a stapedial process.

Trabeculæ, either slender rods with barely enough crest to cover in the optic and oculomotor foramina as in Desmognathus, or solid beams as in Amblystoma, connect the parachordals and otic capsules with the nasal capsules. At its posterior end there are two places at which each trabecula joins the cartilages of the otic region. Of these points of fusion, the ventral, joining the base of the trabecula with the parachordal, is formed early, while the dorsal, joining the trabecular crest with the otic capsule, is a later occurrence. Anteriorly the trabeculæ usually bend inward, and, fusing in the median line into an ethmoid plate, take part in the formation of somewhat complex nasal capsules. But here, again, Desmognathus, with nothing more complex than cornua trabeculæ (Fig. 14, *c*), proves an exception to the general rule.

An antorbital process projects outward and forward from the side of the ventral margin of the trabecula behind the olfactory organ. In some forms it later fuses with the other parts of the nasal capsule. The variety of forms shown by the nasal capsules of the different

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species described renders it difficult to make any accurate statements in regard to these organs which shall apply to the group as a whole. More extended study may show the prevalence of a limited number of these types as is suggested by the similarity between Amblystoma and Plethodon.

Quadrates, arising independently near the anterior end of the otic capsules, later become attached to the rest of the skull by three or four processes. The ascending process unites it with the trabecular crest; the palato-basal with the parachordal; the otic with the otic capsule; and the stapedial process, when present, unites it with the stapes. The palato-basal and otic processes become so intimately related that the blood vessel running between them is the only line of demarcation. A pterygoid process running forward from the body of the quadrate may or may not be present. When present it ends freely in front, not coming in contact with the anterior end of the trabecula and nasal capsule as occurs regularly in the Anura. Ranodon forms the only known exception among the Urodeles to this last statement.

PIPA AMERICANA (Figs. 20–21).

In the single stage of the chondrocranium of Pipa which I have modelled, ossification has proceeded so far that many of the cartilages appear only as remnants of what they were earlier. A brief outline of this skull, however, may serve as a basis from which, with the aid of other studies upon the Anura, especially Gaupp's exhaustive work upon *Rana fusca*, we may contrast the chondrocranium of this group with that of the Urodela.

The occipital processes have fused with the otic capsules and their distal ends have developed into the synotic

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tectum. The parachordals are reduced to a narrow transverse band immediately in front of the base of the occipital arch, and short lateral bands fused with the floors of the otic capsules. The greater part of the wall of the otic capsule is ossified, but enough of the lateral wall remains to show the most important relationships. In this lateral wall of the capsule, further dorsally than in the Urodele skull described, is the fenestra ovalis and in it a small stapes (Fig. 20, *s*) which is connected by a rod running forward and downward with the lateral border of the tympanic annulus (*ta*).

The trabeculæ are small, cylindrical rods extending forward from the ventro-median angles of the anterior ends of the otic capsules and fusing in the broadly expanded ethmoid plate. In the median line the ethmoid plate is continued forward into the nasal septum. At the sides of the posterior end of the septum the ethmoid plate is perforated by the olfactory foramina (*ol*). A triangular lamina cribrosa (*l*) projects outward, downward and forward from each antero-lateral margin of the ethmoid plate. This and the septum with the connecting rods compose the nasal capsules.

From the ventro-lateral margin of the lamina cribrosa (Fig. 21) a slender cartilage projects horizontally inward to beneath the inner border of the lamina where it splits into two cylindrical rods, a dorsal and a ventral. The dorsal rod (*d*) extends forward inward and upward to the antero-dorsal point of the septum, while the ventral rod (*vp*) curves sharply inward, touches the ventral margin of the septum and then, slightly expanding in width, terminates in a process projecting freely forward. A small foramen for the orbito-nasalis, seen only when the skull is viewed from below (*on*), passes beneath the posterior end of the lamina-cribrosa just outside the anterior end of the

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trabecula. The short so-called 'palatine cartilage' is, as has been shown by Gaupp, the homologue of the antorbital process of the Urodela.

The quadrate is situated much nearer the posterior end of the skull than that of the Urodela described. It lies about under the middle of the lateral wall of the otic capsule, to which it is connected by means of a dorsal otic and a ventral palato-basal process. There is no stapedial process connecting the quadrate directly with the stapes, but, as was mentioned above, the stapes is connected with the tympanic annulus which is earlier derived from the quadrate. A slender palato-pterygoid process (*ppt*) projects forward from the body of the quadrate and fuses with the lateral margin of the lamina cribrosa. The relatively posterior position of the quadrate adds proportionately to the length of Meckel's cartilage.

ANURA AND URODELA CONTRASTED.

From a general view of the chondrocrania of these two groups it is seen that, on the whole, in the Anura the width is greater in proportion to its length than in the Urodela. But since there are many very short and broad skulls among the Urodela this distinction is of little value. The closure of the cranial cavity is more complete in the Anura, especially in the ventral region where the basicranial fontanelle, as shown by Gaupp ('93), becomes greatly reduced. Here, too, instead of ending freely, the pterygoid process of the quadrate is attached anteriorly to the ethmoid plate. In these two last mentioned points the Anura show more resemblance to the Selachians than do the Urodela.

We may here insert a few words in regard to the homologies and terminology of the cartilages which have

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been variously called the 'antorbital process' and the 'palatine cartilage.' Gaupp ('91) maintained the homology of the 'antorbital' of the Urodela with the palatine of the Anura. Speaking of this cartilage in Amphiuma, Kingsley ('92) said, "the lower process may retain the name, antorbital, usually applied to it, for Amphiuma presents no evidence that it is the palatine cartilage as Gaupp interprets it." In his final paper on the chondrocranium of Rana, Gaupp ('93) repeats his former position and, stating that he uses the two terms interchangeably, comments upon the above quotation as follows: "Kingsley scheint unter 'Palatine Cartilage' hier etwas Besonderes zu verstehen; was das ist, kann ich aus seinen Angaben nicht ersehen."

There seems to be no doubt as to the correctness of the homology of the cartilages as pointed out by Gaupp. The question here, however, is one of terminology and it is not to be settled by the fact that certain authors have called this cartilage the palatine, but upon the broader grounds of comparative anatomy, and here the question of priority must also be taken into account. The term palatine bone in some of its various modifications was first applied to a bone occurring in the palatal region of the Mammalia, and, in transferring the name to other classes of vertebrates, it is obligatory that it should be given only to those structures which are homologous with the palatine of mammals. That the palatine *bone* of the Amphibia is homologous with the palatine bone in the mammals I do not deny, but I maintain that this cartilaginous process is in no way a palatine process but that rather its relations are with the nasal capsule, and for the following reasons:

In the mammals the palatine bone is regularly enumerated among the membrane bones (Minot '92, *inter alia*) and, so far as I am aware, it has no connection with any

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cartilage. To attempt to homologize a membrane bone with a cartilage is a difficult task. If, however, it be maintained that we have here a case of substitution such as exists in the roofing bones (parietals, frontals, etc.) of the cranium, in which the cartilaginous roof of the brain cavity becomes replaced by the immigration of dermal bones, Ichthyophis throws considerable light upon the question. In this form the palatine bone (part of the maxillopalatine process of the Sarasins), which is distinct in early stages, arises, not in connection with the cartilaginous process in question, but with the nodule of cartilage shown in Figs. 22, 23, and 24, *pc*. In Ichthyophis not only is this true cartilaginous 'palatine' present but the antorbital process occurs as well.

If we adopt the usually accepted homologies (which, however, are not beyond question) the palatine of the higher vertebrates is to be sought in the anterior portion of the upper jaw of the Elasmobranchs, which is accordingly called the palato-pterygo-quadrate or some similar term, implying homologies with the palatine of higher forms. In these very Elasmobranchs, however, the exact homologue of this antorbital process exists, in no way connected with the upper jaw but rather as forming a part of the nasal capsule.

The transformation during metamorphosis from a condition in which the jaw of a small suctorial mouth articulates with the anterior end of the pterygoid cartilage to one in which it reaches back to the body of the quadrate beneath the middle of the otic capsule is one of the most striking characteristics of the Anuran chondrocranium. Another of its distinctive features is found in the auditory apparatus. While in the Urodela the fenestra ovalis may be occupied by a cartilaginous stapes which may or may not be connected with the quadrate by a stapedial process,

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in the Anura we find a much more complicated condition. The fenestra ovalis passes through important changes of form and the stapes comes into connection with a tympanic annulus. But if the tympanic annulus was "originally a postero-superior leaf cut off from the mandibular suspensorium," as stated by Parker and Bettany ('77), the fundamental similarity of the conditions in the two groups is apparent. In connection with this point Gaupp says, "Der vom Quadratum losgelöste knorpelige Annulus tympanicus scheint eine dem Anuren allein zukommende Bildung zu sein." Here, as with the Urodela, the nasal capsule offers little that is of classificatory value.

The chief points of difference between the chondrocranium in the two groups may be tabulated as follows:

URODELA.	ANURA.
1. Both broad and narrow types.	1. Generally, if not always, broad.
2. Pterygoid free in front (except in Ranodon).	2. Pterygoid attached to ethmoid plate.
3. Basi- and supra-cranial fontanelles large.	3. Basi- and supra-cranial fontanelles smaller.
4. No metamorphosis.	4. Very striking metamorphosis.
5. Auditory apparatus comparatively simple.	5. Auditory apparatus, including the tympanic annulus, complex.

ICHTHYOPHIS GLUTINOSUS.

FIRST STAGE (Figs. 22 and 23).—The specimen from which the model for this stage was made was a young embryo still spirally coiled within its membranes. While in some places, more particularly toward the anterior end of the head, the tissue modelled is not true cartilage, the differentiation of all the parts is sufficient to cause little difficulty in distinguishing them.

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The notochord occupies its usual position at the posterior end of the cranium; but, as it passes forward, it bends downward so that its anterior end lies considerably below the general level of the cranial floor. The parachordals are represented only by a narrow band of cartilage connecting the posterior ends of the otic capsules. In the median line the notochord is embedded in this band. At its lateral margin the parachordal band fuses with the occipital process behind and with the otic capsule in front. The dorsal end of the occipital process is fused with the otic capsule. Between these three cartilages is the jugular foramen (*j*).

The otic capsules are longer, narrower and deeper than those of Amblystoma, and, as is usual in the younger stages, they are comparatively widely separated. In the median wall of each capsule are two foramina, a larger anterior and a smaller posterior foramen. The ventrolateral wall of the capsule is largely taken up by the fenestra ovalis along the dorsal part of which lies the stapes. The stapes is continued forward into a process which reaches the posterior surface of the quadrate. This process may retain the name 'stapedial process,' although in this case it is continuous with the stapes rather than with the quadrate. The stapes is perforated in a dorso-ventral direction for the arteria perforans stapedia (Fig. 23, *as*).

Three processes arise from the anterior end of the otic capsule. Two of these, which I shall call the dorsal (*dr*) and ventral (*vr*) trabecular rods, extend forward in the usual positions of the dorsal and ventral margins of the trabecula. The third, and relatively much shorter process is attached posteriorly to the otic capsule just below the end of the dorsal trabecular rod. Curving downward and forward it fuses with the ventral trabecular rod. In the posterior end of the ventral trabecular rod there is a small

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foramen traversed by a nerve (apparently the palatine). This foramen does not appear in the later stages modelled but I am unable to give the details of the disappearance.

After passing forward separately to the orbital region, the dorsal and ventral trabecular rods of each side are connected by two narrow bands of cartilage, a post-orbital (*pob*) and a pre-orbital (*prb*) between which the elongated optic foramen (*of*) is enclosed. Beginning in the region of the post-orbital band the dorsal and ventral trabecular rods of each side, which have thus far been approximately parallel, diverge in a horizontal direction. The dorsal rod curves first outward and then inward, giving off ventrally a plate-like lamina cribrosa near its anterior end. The two ventral rods bend inward to the median line where they unite to form a small ethmoid plate. Just behind their point of fusion each ventral rod gives off a ventro-lateral process which underlies the posterior end of the olfactory vesicle. From the anterior margin of the pre-orbital band of cartilage an antorbital process (Fig. 23, *anp*) extends outward and forward towards the ventral portion of the lamina cribrosa.

The quadrate is composed of a body, and ascending and pterygoid processes. The body is small and stands out from the side of the ventral trabecular rod below the anterior end of the ear capsule, with which it is not directly connected. The ascending process passes upward and forward and unites with the dorsal trabecular rod a little in front of the ear capsule. The pterygoid process (*pt*) is composed of two parts, a short proximal portion which projects forward from the body, and an isolated portion which later becomes the distal end of the process. This method of development of the pterygoid is the same as that mentioned by Gaupp ('91) for Siredon. A short dis-

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tance in front of the distal portion of the pterygoid is another isolated rod of cartilage which runs in a direction diagonal to that of the pterygoid process. This is the palatine cartilage (*pc*).

Meckel's cartilage articulates with the ventral surface of the body of the quadrate. Anteriorly the cartilages of the two sides are still separated. They project backward behind the point of articulation with the quadrate nearly as far as the posterior end of the stapes (*a*).

SECOND STAGE (Figs. 24–26).—The parachordals and occipital processes are in the same condition as before, there being no trace of the formation of a synotic tectum. The notochord has entirely disappeared from the head region. The median wall of the otic capsule is more complete than it was in the first stage (Fig. 25). What was then the large anterior foramen is now divided into a dorsal foramen for the endolymphatic duct (*ef*) and a large ventral foramen for the auditory and facial nerves. The floor of the capsule is now composed of a median and a more lateral rod between which a fontanelle is enclosed. The stapes and fenestra ovalis are in the same condition as in the preceding stage.

The rod described in the first stage as connecting the anterior end of the otic capsule with the ventral trabecular rod now has a nearly vertical direction, the ventral end being relatively more posterior in position than before. As far forward as the orbital region there are no other noteworthy changes. In the nasal region, however, important changes have occurred. Instead of the transversely expanded nasal region of the earlier stage, we now find the anterior ends of the dorsal trabecular rods folded inward toward the nasal septum and forming a roof over the sides of the olfactory organs. By this movement the

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lamina cribrosa is brought into its usual position. Its distal end is fused with that of the antorbital process thus enclosing the orbito-nasal foramen (Figs. 24 and 26, *on*).

The ethmoid plate is larger in both directions than in the first stage, and in the median line upon its anterior half arises the nasal septum (*ns*). In front, upon the sides of the base of the septum, the ethmoid plate terminates in short free processes. The nasal septum is divided anteriorly into three parts, a short median process which projects freely forward, and two lateral bands which curve forward and outward. At its most anterior point each of these bands divides into a dorsal and a ventral process. These extend backward along the lateral surface of the olfactory organ and fuse with the outer end of the cartilage mentioned in the first stage as arising from near the anterior end of the ventral trabecular rod. Where these three processes meet a plate of cartilage is formed which lies below the lamina cribrosa and is connected with it by a short narrow band. No tectal cartilage is formed in the chondrocranium of Ichthyophis.

As a result of ossification the ascending process of the quadrate has lost its cartilaginous connection with the dorsal trabecular rod (Fig. 24), and the parts of the pterygoid process are now united into one continuous rod. The body of the quadrate remains essentially unchanged, it having neither otic nor palato-basal process. The two cartilages of Meckel are now confluent in front, and the palatine cartilage still remains isolated from the rest of the chondrocranium. It appears that the ancestors of the Batrachia had a palato-pterygo-quadrate cartilage similar to that found in sharks. Of these cartilages the Urodeles as a rule retain only the pterygoid and quadrate portions. The Cæcilians have these two parts and an isolated palatine portion, while in the Anura all three parts are united

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in one rod which is joined in front to the antorbital process.

THE CÆCILIAN CHONDROCRANIUM.

There are two views according to which the Cæcilians are related to Amphiuma. According to one — the theory of Cope ('89[a]) — the Cæcilians are the extreme of a line of degeneration from the typical Urodele stock and Amphiuma is one of the intermediates of the series nearest to the Gymnophiona. Indeed, Cope goes so far as to make the Cæcilians merely a family of the Urodeles. The other view is that of the cousins Sarasin who hold that Amphiuma is a neotenic Cæcilian, a larval Cæcilian become sexually mature while retaining their branchial respiration.

According to the first view Amphiuma, and to a less extent the rest of the Urodeles, must be closely similar in cranial as well as other structures to the young Cæcilian. Farther, if we find that Amphiuma and the Urodeles have lost certain features which belonged to the ancestral Craniota, the retention of these characters by the Cæcilians would be an argument against the line of descent advocated. The view of the Sarasins presents even more difficulties for we have both horns of the dilemma. If Amphiuma be merely a Cæcilian arrested in a larval condition, then we have to say either that Amphiuma is not related to the remaining Urodeles or that they have all sprung from a Cæcilian ancestry. The objections to the second view are so many and so weighty that we think no one would care to defend it. The limbs alone are enough to set it aside. As to the other horn, it would seem that all the evidence we have regarding adult structure and development as well goes to show that Amphiuma is far more closely allied to the other Urodeles than it is to the Cæcilians, while the same matter of limbs, weak though

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they be in Amphiuma, throws the whole view out of court.

There remains then but the view of Cope, and this is to be tested by seeing if there be features in the Cæcilians which must have been inherited and which could not have been inherited from an Urodele ancestor.

The parachordals of Ichthyophis are smaller than those of any other form studied. The nearest approach to them is found in Desmognathus where there are bands, not present in Ichthyophis, connecting the anterior end of the notochord with the otic capsules. No synotic tectum is formed in Ichthyophis, though at one period in the development of the skull small crests on the dorso-median walls of the otic capsules represent the first steps in the formation of a tectum. This appearance, however, is slight and but transitory.

There is a difference between the manner of development of the trabeculæ of Ichthyophis and those of the other Batrachia described. Instead of being developed by the successive formations of a ventral rod, a trabecular crest and a connective rod uniting the crest to the otic capsule, we have the dorsal rod developing simultaneously with the ventral rod and equally well chondrified. The dorsal rod, separated as it is from the ventral rod and attached to the anterior point of the otic capsule, somewhat resembles the supraorbital band of fishes. But the fusion of the ascending process of the quadrate with the dorsal rod and the relations of the two trabecular rods anteriorly are clearly Urodelan characters. The quadrate is peculiar, however, in having no otic or palato-basal processes. Aside from the ascending process and stapes it is entirely separated from the rest of the skull. Its position is the same as that of the Urodeles. The stapes is perforated for the stapedial artery.

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But more important than any of the features mentioned above is the existence of an isolated palatine cartilage. This is especially noteworthy since it seems to furnish strong evidence in opposition to the theory of the Urodelan ancestry of the Cæcilians. Ranodon is the only Urodele which possesses that portion of the palato-pterygoid arch which may be considered to correspond to the palatine cartilage of Ichthyophis, while in Amphiuma there is not the slightest trace of it. We may therefore conclude that the condition found in Ichthyophis was not derived from an Urodelan ancestor but from some more primitive form.

The articular process of Meckel's cartilage is unusually long in Ichthyophis. The nasal capsules, while differing from all the others described, have no features of sufficient importance to be of any especial classificatory value.

The evidence which I have found, chiefly from a study of the chondrocranium, appears to me to be against associating the Cæcilians with any of the Urodeles and in favor of keeping them in a distinct group coördinate with the Urodela and Anura.

POLYPTERUS BICHIR (Fig. 27).

In 1892 the late H. B. Pollard kindly allowed Dr. Kingsley to trace the outlines of the cartilages in the sections of the head of his youngest Polypterus. From these drawings I have made the chondrocranium in wax. Since the skull of this same specimen has already been described and figured by Pollard ('91) I shall deal chiefly with points of value from a comparative standpoint. For further details in regard to the relations of the chondrocranium to the rest of the head, reference should be made to Pollard's paper which contains a

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dorsal view of the skull and drawings of sections through various parts of the head.

No cartilaginous occipital arch is present, owing, apparently, to ossification. The otic capsule is large and selachian-like in form. In its postero-lateral wall there is a large aperture exposing portions of the posterior and horizontal canals. This also is probably due to ossification. A small remnant of the hyomandibular cartilage (*h*) lies in a groove in the dorso-lateral surface of the capsule. That it formerly reached down as far as the posterior end of the pterygo-quadrate cartilage is shown by the figures of Pollard and others.

A thick synotic tectum covers the brain cavity in the posterior two-thirds of the otic region. There are indications of a medial capsular wall separating the brain cavity from the cavity of the capsule at its posterior and anterior ends, but the greater part of the space is entirely open. The floors of the capsules are continuous with the basilar plate which slightly exceeds the synotic tectum in extent. A peculiar rod of cartilage (*bo*) projects a short distance backward from beneath the middle of the basilar plate. At the anterior end of the capsules there are upon each side two foramina and a deep groove which is now open in front and apparently represents another foramen the anterior wall of which is ossified. A short bar of cartilage passes across the external opening of the posterior of the two foramina, dividing it here into two. The unossified posterior end of the supraorbital band remains as a solid lateral projection upon the anterior end of the otic capsule.

There is a complete separation of the chondrocranial elements of the otic region from those of the orbital and nasal regions. The supraorbital band (*sb*) passes anteriorly into a broad tegmen cranii (*tc*) which covers over

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the anterior end of the cranial cavity and continues forward into the roof of the nasal capsules. Ventrally a solid plate of cartilage (*t*), the trabecular plate, forms a continuous floor beneath the anterior end of the cranial cavity and the nasal capsules, and projects forwards as a short and rather blunt rostrum (*r*). A small isolated plate of cartilage (*tc*) occupies the middle of the supracranial fontanelle, a remnant, as Pollard suggests, of a primitively complete tegmen cranii.

The nasal capsule consists of a large cavity enclosed by simple, broad plates of cartilage. Its floor and roof are connected by a tall septum medially and two bands laterally. The posterior of these two bands marks the boundary between nasal capsule and cranial cavity. There are three large apertures in the capsule walls: behind, the olfactory foramen; in front, the foramen for the nasal duct (*nl*); and between them a third in the lateral wall. Besides these there are two small foramina in the border of the nasal roof, the 'canalis ethmoidalis' (*ec*) and the 'canalis preorbitalis' (*prc*). Dorsally these two are connected by a deep groove.

The anterior end of the palato-pterygo-quadrate cartilage (*ppt*) is applied to the ventro-lateral surface of the nasal capsule. From here it passes backward as a broadening band to a point beneath the outer wall of the otic capsule and the hyomandibular cartilage. In passing from in front backward it twists from an approximately horizontal to a nearly vertical plane.

THE TROUT (*Salmo fontinalis*), (Figs. 28–29).

For a representative of the Teleostean skull I have modelled the chondrocranium of a trout embryo twenty-two mm. in length. The occipital arch is fused with the

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otic capsules leaving no suggestion of their former separation, except in the jugular foramina (Fig. 29 *j*). The notochord extends forward beyond the middle of the otic region. Its sides are embraced by the two halves of the basilar plate. At its apex it projects freely forward for a short distance. Except for a small fontanelle (*f*), the basilar plate is continuous with the walls of the otic capsules which are united above by a broad, arched synotic tectum. The positions of the semicircular canals are clearly indicated in the external surface of the otic capsules. No median wall separates the cavity of the ear from that of the brain. In front and a little below the jugular foramen there is another smaller foramen through which the ninth nerve (*ix*) passes out of the cranium. Farther forward there are three more apertures in the ventral wall of the capsule. The posterior of these is the fontanelle mentioned above. The middle one of the three is small and is traversed by the hyomandibular branch of the facial nerve (*hy*). The anterior foramen is for the exit of a branch of the jugular vein (*jv*).

The basilar plate is continued forward into a trabecula upon either side. These extend separately to a point in front of the hypophysis and then unite along the median line in a narrow trabecular band. This band has the shape of an inverted trough and reaches to the anterior end of the skull, expanding in the nasal region into the ethmoid plate which forms the floor of the nasal capsules. The palatine branch of the seventh nerve (Fig. 28, *pal*) passes downward through a foramen in the posterior end of the trabecula. Two slender supraorbital bands (*sb*) arise from the anterior ends of the otic capsules and curve forward and inward, until about half way from the otic to the nasal region, where they enter the margins of the arched tegmen cranii which covers the anterior end of the

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cranial cavity. This cranial roof is fused anteriorly with the dorsal end of the nasal septum (Fig. 28, *ns*). In its anterior end there are three apertures, a median fontanelle and two small lateral foramina, through each of which passes a branch of the ophthalmicus superficialis (*rs*). A band of cartilage connecting the tegmen cranii and the dorsal end of the septum with the lateral border of the ethmoid plate separates the nasal region from the cranial cavity. There is no cartilaginous roof or lateral wall to the nasal capsule. The septum is thick and slightly expanded dorsally and in front where it ends bluntly.

The anterior end of the pterygo-quadrate cartilage is applied to the ventro-lateral margin of the ethmoid plate. From here it extends backward as a slender rod to beneath the anterior end of the otic capsule where it broadens into an irregular plate with an articular process ventrally for the attachment of Meckel's cartilage. Its posterior end is connected with the otic capsule by means of the plate-like hyomandibular cartilage (*h*). The dorsal margin of this cartilage, the hyomandibular, lies closely pressed against the external surface of the otic capsule just beneath the horizontal canal. It is broad and thin above and narrower and thicker below. From its ventral end a long rod-like process runs forward beneath the posterior end of the pterygo-quadrate, reaching almost to the point of articulation with Meckel's cartilage. The hyomandibular branch of the seventh nerve passes through a foramen just above the middle of this cartilage (*hy*).

THE CHONDROCRANIUM IN THE FISHES.

The chondrocrania of the two types of this group which have been described have many features in common, and it seems probable that a comparison of corres-

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ponding stages in the development of the two forms would show a still more marked similarity. The otic capsules are connected dorsally by a solid synotic tectum and ventrally by an unbroken basilar plate formed by the fusion of the parachordals around the anterior end of the notochord. The median wall of the otic capsule is either absent or but slightly developed. Neither fenestra ovalis nor stapes occurs.

The trabeculæ unite ventrally into a median band in front of the hypophysis and continue forward to the end of the skull. At its anterior end the trabecular band broadens out into the ethmoid plate which forms the floor of the nasal capsules. Supraorbital bands extend forward from the anterior ends of the otic capsules to the lateral margins of the tegmen cranii which roofs over the anterior portion of the brain cavity.

The palato-pterygo-quadrate cartilage extends from the lateral margin of the ethmoid plate backward to beneath the anterior end of the otic capsule. Its posterior end is supported to a greater or less degree by the ventral end of the hyomandibular cartilage which has its dorsal end closely applied against the outer wall of the otic capsule. Meckel's cartilage articulates with the ventral surface of the quadrate portion of the palato-pterygo-quadrate cartilage.

In discussing the relations of Polypterus to the Batrachia, Pollard said, "On comparing the primordial cranium of a young Polypterus with that of Urodeles, the general resemblance is seen to be so great that an anatomist seeing it alone for the first time would certainly place it among the latter." Considering the features which distinguish the chondrocranium of Polypterus in common with the rest of the Fishes from that of the Batrachia, as outlined in the preceding pages, so great a similarity can

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hardly be admitted to exist. The great similarity pointed out above between the skulls of Polypterus and the trout and the many points in which they differ from the typical skull of the Batrachia cause me to feel considerable hesitancy about accepting the theory of the Crossopterygian ancestry of the Batrachia. But, while the presence in Polypterus of a large hyomandibular cartilage, a quadrate well removed from the otic capsule and a strong supraorbital band, as well as the absence of any fenestra ovalis or stapes, will remain important obstacles to this view until transitional stages are found, perhaps these difficulties are less than those attending the Dipnoan theory. Attention may also be called to the fact that in Polypterus there is a limited median capsular wall, which is not found in either the trout or Protopterus but which regularly occurs in the Batrachia.

PROTOPTERUS ANNECTENS (Figs. 30–32).

A model of the chondrocranium of Protopterus gives us a basis from which to compare the Dipnoi on the one hand with the Batrachia, to which they have been considered to be closely related, and on the other to the Teleosts and Ganoids.

Viewed as a whole the massive character of many of the cartilages of this skull is a most striking feature. Ossification in the occipital region somewhat obscures the relations between the skull and the first vertebra. The occipital processes are fused with the otic capsules leaving large jugular foramina in the usual position. The remnant of the notochord is imbedded in a solid parachordal plate extending from the posterior end of the skull forward to the middle of the otic region. On each side of the median line at the anterior end of the parachordal plate is an

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elongate fontanelle (Fig. 32, *f*). The walls of the otic capsules are continuous ventrally with the parachordal plate and dorsally with a strong synotic tectum. From the external margin of the otic capsule a broad ledge of cartilage projects horizontally outward, widening as it passes from behind forward where it terminates abruptly. There is no median capsular wall.

Band-like trabeculæ extend forward along the sides of the brain from the dorsal anterior end of the otic capsules to the optic region where they bend around ventrally to form a large ethmoid plate. From the dorsal margin of the anterior end of each trabecula a peculiarly bent antorbital process (*anp*) arises. It projects forward and outward, coming into close proximity to, but not fusing with the posterior end of the nasal capsule, and then it bends backward, running along the margin of the upper lip. The ethmoid plate narrows down in passing from behind forward, and terminates in two processes which bend sharply upward and fuse with the posterior end of the nasal septum. Between these two terminal processes there is an oval fontanelle.

The nasal capsule is a very peculiar one. The septum is a thin dorsal plate behind, but in front it becomes a solid cylindrical mass of cartilage projecting ventrally between the olfactory organs. The transition from one condition to the other is very abrupt. In front the septum ends in two short laterally directed processes. Six bands of cartilage extend outward and downward from the median septum to a curved marginal band (*mr*). Between these bands five apertures of various shapes and sizes are enclosed. The anterior of the six transverse bands projects somewhat beyond its point of fusion with the marginal band. As is seen in the ventral view (Fig. 32) a curved process extends inward and upward from the inner

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border of the marginal band. Its dorsal end is free. Just in front of the bend of the antorbital process is an isolated strip of cartilage occupying a diagonal position, one end being dorso-medial and the other ventro-lateral. A small cylindrical rod (*tc*) extends backward in the median line from the posterior end of the nasal septum and ends freely above the brain, a remnant of the ancestrally complete tegmen cranii.

The quadrate has its base firmly fused with the otic capsule and trabecula. It is a solid mass projecting downward and forward, and presents upon its anterior end a large articular surface for the enormous posterior end of Meckel's cartilage (Fig. 30). Except for a short distance in front of its point of articulation, Meckel's cartilage is of only ordinary size. There are upon each side of the lower jaw three labial cartilages (*lc*). As shown in the figure the posterior of these is separated from the jaw and divided into two parts, but this occurred upon the right side only. By mistake the anterior end of the lower jaw was drawn nearly straight instead of curved sharply upward as it should have been.

The ninth nerve (*ix*) passes out through a small foramen a short distance in front of the jugular foramen. Five foramina grouped about the anterior end of the otic capsule open upon the dorso-lateral surface of the skull. I have designated the nerves passing through these foramina in accordance with the work of Pinkus ('94). The third nerve passes through a small foramen (Fig. 30, *oc*) near the dorsal margin of the trabecula. Just below the foramen for the third is a larger one for the ramus ophthalmicus profundus of the fifth (*rp*), and still lower is another for the ramus maxillaris of the fifth (*rm*). A short distance behind this foramen are the openings of the other two lying close together, one above the other. The

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more dorsal of the two is traversed by two nerves, the ramus lateralis facialis of the seventh (*rl*) and the ramus ophthalmicus superficialis of the fifth (*rs*). The more ventral foramen is for a blood vessel (*b*).

Three foramina open upon the ventral surface of the skull in this same region (Fig. 32). Of these the anterior and smallest is for the ramus palatinus superior (*rps*). The other two openings are close together. The more median is for the main trunk of the seventh (*vii*) and the ramus palatinus inferior (*rpi*). The more lateral opening is the ventral end of the foramen for the blood vessel mentioned above.

THE CHONDROCRANIUM IN THE DIPNOI.

A comparison of the chondrocranium of Protopterus with those of the Batrachia and Fishes at once reveals its unique character. While resembling the typical chondrocranium of each of these groups in some respects, taken as a whole it is very different from either. The large otic capsule, with thick walls and separate foramen for the ninth nerve, and without a median wall or fenestra ovalis, greatly resembles the capsule of Fishes. But the suspensorial apparatus is entirely different from that of most Fishes and very similar to that of the Batrachia, that is to say, it is autostylic. According to Huxley ('76) this condition is also found in the Chimæroids and Marsipobranchii, but in none of the other Fishes. This is undoubtedly the strongest point of resemblance between the chondrocrania of the Dipnoi and Batrachia. And here the theory of the Dipnoan ancestry of the Batrachia is decidedly at an advantage over the Crossopterygian theory. But this similarity of the otic relations of the quadrate in these two forms is counterbalanced by differ-

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ences in other respects. The absence of a palato-pterygoid cartilage is an especially noteworthy feature in this connection which indicates the highly specialized nature of this skull and renders it impossible to consider it a very near approach to the ancestral Batrachian skull.

The trabeculæ are unlike both those of the Fishes and those of the Batrachia. When their posterior ends are compared with the chondrocranium of the former group they seem rather to represent the supraorbital bands, arising as they do from the antero-dorsal surface of the otic capsules. But in passing forward, instead of curving up over the eye as supraorbital bands should do, they curve downward and fuse at their anterior ends into an ethmoid plate very much as occurs in the Batrachia. The antorbital process arises from the dorsal margin of the trabecula, a condition found in none of the other forms studied; and the ethmoid plate, instead of continuing forward to form a floor beneath the nasal capsules, as is the general method in both Fishes and Batrachia, curves sharply upward at its anterior end and fuses with the dorsally situated posterior end of the nasal septum. The possession of a remnant of the tegmen cranii is another fish-like character.

As was mentioned in the discussion of the chondrocranium of Necturus, there is some resemblance between the nasal capsules of that form and those of Protopterus. But, in view of the differences between the nasal capsules of the various forms of Urodeles themselves and considering the many important points of difference in other parts of the skull, it seems to me an entirely unwarrantable conclusion to assume any phyletic relationship between these two forms upon this account.

Günther has described the skull of Ceratodus as consisting "of a completely closed inner cartilaginous

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capsule and an outer incomplete osseous case, to which, again, some other cartilaginous elements are appended." From this description and from the fact that a cartilage considered to be a remnant of the hyomandibular has been found in Ceratodus it seems probable that the chondrocranium of this form resembles that of the Fishes more than does that of Protopterus. But the evidence from the chondrocranium of Protopterus, in so far as it may be considered to have value in determining the position of the Dipnoi as a whole, appears to me to be entirely in agreement with the conclusion of W. N. Parker that, "it is certainly inadvisable to retain the Dipnoi among the Fishes, as is still done by some zoologists, and it would be still more undesirable to place them with the Amphibia." It is to be remembered, however, that Protopterus is one of the more specialized forms of the group.

POSTSCRIPT.

Since the foregoing article passed into the hands of the printer a paper by Miss Platt[1] has appeared which deals with the development of the cartilaginous skull of Necturus, giving special attention to the origin of the procartilage cells. In the main our results in regard to the fully chondrified parts entirely agree. Miss Platt finds, however, that in Necturus the number of cartilages arising independently is considerably larger than that described above for Amblystoma. Of these the synotic tectum ('tectum interoccipitale'), the trabecular crest, and the ethmoid ('internasal') plate are of particular interest

[1] Platt, J. B. The development of the cartilaginous skull and of the branchial and hypoglossal musculature in Necturus. Morph. Jahrbuch. XXV, p. 377. 1897.

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from the fact that I have not found them to appear as independent cartilages in any of the forms studied. This may, in some cases, be due to the fact that the independent condition is limited to the pro-cartilage stages or to the incompleteness of my series of embryos. But I feel confident that the parts mentioned do not appear as independent cartilages in Amblystoma. The existence of such a condition as that shown in Fig. 18, where there is no sign of cartilage near the median line, and the appearance of a complete tectum in an embryo but little older form the basis of my conclusions in regard to the synotic tectum. My evidence as to the formation of the trabecular crests and the ethmoid plate is of the same nature and shows them to be outgrowths from the primitive trabeculæ.

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EXPLANATION OF THE FIGURES.

REFERENCE LETTERS.

a. Angular process.
a n p. Antorbital process.
a p. Ascending process.
a s. Arteria perforans stapedia.

b. Foramen for blood vessel.
b o. Basi-occipital cartilage.
b q. Body of quadrate.

c. Cornu trabeculæ.

d. Dorsal nasal process.
d p. Descending process of quadrate.
d r. Dorsal trabecular rod.

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e. Ethmoid plate.
e c. Ethmoid canal.
e f. Endolymphatic foramen.

f. Fontanelle.
f o. Fenestra ovalis.

h. Hyomandibular cartilage.
h y. Foramen for hyomandibular branch of seventh nerve

i x. Foramen for ninth nerve.

j. Jugular foramen.
j v. Foramen for branch of jugular vein.

l. Lamina cribrosa.
l c. Labial cartilage.
l o c. Lateral occipital crest.

m. Meckel's cartilage.
m r. Marginal rod.

n. Notochord.
n c. Nasal capsule.
n i. Foramen for branch of nasalis internus.
n l. Nostril.
n s. Nasal septum.

o. Otic capsule.
o c. Oculomotor foramen.
o c p. Occipital process.
o f. Optic foramen.
o l. Olfactory foramen.
o n. Orbito-nasal foramen.
o p. Otic process.

p. Parachordal.
p a l. Palatine foramen.
p b. Palato-basal process.
p c. Palatine cartilage.
p f. Perilymphatic foramen.
p o b. Postorbital band.
p p t. Palato-pterygo-quadrate cartilage.
p r b. Preorbital band.
p r c. Preorbital canal.
p t. Pterygoid process.

q. Quadrate.

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r. Rostrum.
r l. Foramen for ramus lateralis facialis of the seventh nerve.
r m. Foramen for ramus maxillaris of fifth nerve.
r n. Foramen for ramus mandibularis of fifth nerve.
r p. Foramen for ramus ophthalmicus profundus of fifth nerve.
r p i. Foramen for ramus palatinus inferior.
r p s. Foramen for ramus palatinus superior.
r s. Foramen for ramus ophthalmicus superficialis of fifth.

s. Stapes.
s b. Supraorbital band.
s p. Stapedial process.
s t. Synotic tectum.
s u. Support of balancer.

t. Trabecula.
t a. Tympanic annulus.
t c. Tegmen cranii.
t e. Tectal cartilage.
t m. Taenia tecti medialis.
tr c. Trabecular crest.

v. Foramen for branch of fifth nerve.
vii. Foramen for branch of seventh nerve.
viii. Foramen for branch of eighth nerve.
v p. Ventral nasal process.
v r. Ventral trabecular rod.

EXPLANATION OF PLATES.

Fig. 1. Side view of model from *Amblystoma punctata*, ten mm. long.
Fig. 2. Dorsal view of same.
Fig. 3. Dorsal view of model from *Amblystoma punctata*, eleven mm. long.
Fig. 4. Side view of model from *Amblystoma punctata*, twelve mm. long.
Fig. 5. Dorsal view of same.
Fig. 6. Ventral view of same.
Fig. 7. Dorso-median view of otic capsule of same.
Fig. 8. Side view of model from *Amblystoma jeffersoniana*, thirty-nine mm. long.
Fig. 9. Dorsal view of same.

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Fig. 10. Ventral view of same.
Fig. 11. Median view of otic capsule of same.
Fig. 12. Dorsal view of model from *Amblystoma punctata*, sixty-nine mm. long.
Fig. 13. Ventral view of same.
Fig. 14. Dorsal view of model from *Desmognathus fusca*, twenty mm. long.
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Fig. 21. Ventral view of nasal region of same.
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Fig. 31. Dorsal view of same.
Fig. 32. Ventral view of same.

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The following list includes the papers issued from the Biological Laboratories of Tufts College:

No. 1. The head of an embryo Amphiuma. By J. S. Kingsley. American Naturalist, vol. xxvi, pp. 671–680. 1892.

No. 2. The embryology of Limulus. By J. S. Kingsley. Journal of Morphology, vol. vii, pp. 35–68. 2 pls. 1892.

No. 3. The embryology of Limulus. Part II. By J. S. Kingsley. Journal of Morphology, vol. viii, pp. 195–268. 4 pls. 1893.

No. 4. Ectodermic origin of the cartilages of the head. By Julia B. Platt. Anatomischer Anzeiger, Bd. viii, pp. 506–509. 1893. Tufts College Studies, No. 1, pp. 11–13. 1894.

No. 5. The anterior cranial nerves of Pipa americana. By George A. Arnold. Bulletin of the Essex Institute, vol. xxvi, pp. 1–9. 1893. Tufts College Studies, No. 1, pp. 1–9. 1 pl. 1894.

No. 6. The classification of the Arthropoda. By J. S. Kingsley. American Naturalist, vol. xxviii, pp. 118–135 and 220–235. 1894. Tufts College Studies No. 1, pp. 15–48. 1894.

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No. 12. The morphology and classification of the Pauropoda, with notes on the morphology of the Diplopoda. By Frederick C. Kenyon. Tufts College Studies, No. 4, pp. 77–146. 4 pls. 1895.

No. 13. On three points in the nervous anatomy of Amphibians. By J. S. Kingsley. Journal of Comparative Neurology, vol. vi, pp. 54–58. 1896.

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No. 17. The nasal organs of Pipa americana. By Irving Reed Bancroft. Bulletin Essex Institute, vol xxvii, pp. 101–107. 2 pls. 1897.

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THE OSSICULA AUDITUS.

By J. S. Kingsley.

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The studies described in the following pages were undertaken by Dr. W. H. Ruddick and myself, with some hopes of throwing light upon the vexed problems connected with the ear bones of the mammals and the fate of the quadrate in that group. Our results have in part been published in a joint paper (Kingsley and Ruddick, '99), while all additions to the facts and opinions there expressed as exhibited in the present article are my own. Dr. Ruddick has been drawn off to the investigations of some of the other problems which have been suggested by points discovered during the preparation of this paper.

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Notwithstanding the fact that several students who have interested themselves in this ear bone problem have announced that they have settled the matter, the great trouble has been that it has been "settled" in two ways, and these so diverse that reconciliation is almost out of the question. Certainly both views have arguments in their favor, and as certainly both views cannot be perfectly correct.

A detailed analysis of the somewhat extensive literature is not necessary here, since almost every previous student has given such reviews. The general conclusions of most authorities are given in tabular form below, but a few words of explanation will serve to introduce the problems concerned to the general student.

In the lower fish-like vertebrates the sides of the pharyngeal region is perforated by pairs of gill slits, the first of which, in the elasmobranchs and some ganoids, differs from the rest, and is here known as the spiracular cleft. Between each two gill clefts of a side are skeletal elements known as the branchial arches, the arch just behind the spiracle bearing the special name of hyoid. In front of the spiracle and between it and the mouth (often regarded as formed by the coalescence of a pair of gill slits) is the skeletal arch, which in the elasmobranch forms the upper and lower jaws. The half in the lower jaw is known as Meckel's cartilage; the upper as the pterygoquadrate. In most sharks the pterygoquadrate is suspended from the skull, in front by means of ligaments, while behind, the upper half of the hyoid arch, the so-called hyomandibular intervenes between the cranium and the angle of the jaw. With the appearance of bone, as in the teleosts, the pterygoquadrate ossifies as a quadrate bone behind, and one or more bones in front, which are grouped as the pterygoids. In the hyomandibular cartilage there appears an upper hyomandibular and a lower or symplectic ossification, these two forming the suspensor of the jaws. The lower jaw now articulates with the quadrate, and the jaw itself consists of a number of membrane bones—dentary, splenial, angulare, etc.—arranged around Meckel's cartilage,

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while the proximal end of the cartilage may ossify as a distinct bone, the articulare.

From the amphibia upward the symplectic and hyomandibular have disappeared from their position as suspensors, and in amphibia and sauropsida the quadrate serves to suspend the lower jaw from the cranium, with which it may be either freely or firmly articulated. In the urodeles and cæcilians the spiracular cleft disappears in the course of development, but in anura, sauropsida and mammals it extends outwards, in front of and beneath the otic capsule, as a slender canal, the Eustachian tube, which expands distally into a larger cavity, the tympanum, separated from the external world by a thin tympanic membrane, which may be placed either on the surface of the head or at the bottom of an ectodermic inpushing, the external auditory meatus.*

In these forms with a developed tympanum, sound waves are conducted across the tympanic cavity from the tympanic membrane to an opening in the otic capsule—the fenestra ovalis—by means of one or more skeletal elements, the ossicula auditus. In the anura and the sauropsida this sound-conducting chain (columella) may be described as consisting of an expanded plate, the stapes, which is held by membrane in the fenestra ovalis, and leading outwards from it a slender rod, the distal end of which, the extracolumella, is inserted in the tympanic membrane. In the mammals, on the other hand, a chain of three bones replaces the two of the forms just mentioned. These are a stapes, placed as in those animals; next, an incus; and externally, and inserted in the tympanic membrane, the malleus. In these mammals, also, the quadrate has disappeared from the suspensor apparatus, and the lower jaw articulates directly with the skull at the glenoid fossa, in front of the otic capsule.

*The above is the usual account of the homologies of the Eustachian tube and tympanic cavity, and one which fits best with morphological facts; but it must be remembered that this has been questioned by Hunt and Urbantschitsch. The matter, however, will be referred to again in connection with the discussion of a segment intermediate in position between hyoid and mandibular.

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The problems may be stated briefly as follows: (1) What has been the fate of the hyomandibular and symplectic in the non-piscine vertebrates? (2) In what way has the stapes arisen? (3) What homologies can be traced between the ossicula auditus of the mammals and those of anura and sauropsida? and (4), What has become of the quadrate in the mammalia? I have tabulated below the conclusions to which some of the various students of this problem have come. While the list is not complete, it serves to illustrate the great diversity of opinion which exists.

	QUADRATE.	HYOMANDIBULA.	STAPES.	INCUS.	MALLEUS.
Albrecht, 83	Glenoid region				
Balfour, 81	Malleus			Prox. end of hyoid	Quadrate
Baraldi, 77	Incus	Stapes	Hyomandibula	Quadrate	Articulare
Baumgarten, 92			Hyoid arch	Mandibular arch	Mandibular arch
Baur, 87	Glenoid region				Distal end of columella
Baur, 89	Glenoid region		Opisthotic		
Broman, 98			Hyoid arch	Meckel's cartilage	Meckel's cartilage
Claus, 87	Incus	Stapes	Hyomandibula	Quadrate	Articulare
Cope, 85	Glenoid region		Around stapedial Artery	Epicolumella*	Extracolumella
Dollo, 83	Glenoid region		Columellar tract	Columellar tract	Columellar tract
Dreyfuss, 93			First or second arches	Meckelian	Meckelian
Fraser, 83			Periarterial	Hyoid arch	Mandibular arch
Gegenbaur, 70, 78, 98	Incus	Stapes	Hyomandibula	Quadrate	Articulare
Günther, 42			Mandibular arch	Mandibular arch	Mandibular arch
Gradenigo, 87		Stapes in part	Otic capsule plus Hyomandibula	Meckel's cartilage	Meckel's cartilage
Gadow, 88	Tympanic framework	Ossicula auditus	Hyomandibula	Hyomandibula	Hyomandibula Extracolumella
Hasse, 73	Incus	Stapes	Hyomandibula	Quadrate	Prox. end Meckel's
Hertwig, O., 96			Uncertain	Prox. end Meckel's	Articulare
Hertwig, R., 92	Incus	Stapes	Hyomandibula	Quadrate	Articulare

*Cope's 'epicolumella' was based upon a supposed columella of Clepsydrops, but Baur and Case ('97, p. 116) say that this columella was in reality a rib, a view which seems probable.

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Hoffmann, 90	Incus	Hyostapes		Quadrate	Articulare
Huxley, 64	Incus			Quadrate	Meckel's cart.
" 67	Incus			Quadrate	Articulare
" 69		Incus	Hyoid	Hyomandibula	
" 71	Malleus	Incus	Hyoid	Hyomandibula	Quadrate
Killian, 90	Incus		Prox. end columella	Quadrate	
Kölliker, 79	Incus		Otic capsule	Quadrate	Articulare
Köstlein, 84	Glenoid reg'n				
Kükenthal, 96	Incus	Stapes	Hyomandibula	Quadrate	Articulare
Marshall, 93			Otic capsule	Uncertain	Uncertain
Minot, 92	Incus		Ossification in fenestra ovalis	Quadrate*	Prox. end Meckel's
Van Noorden, 87			Otic capsule plus hyoid	Meckelian	Meckelian
Parker, 74	Malleus	Incus		Hyomandibula	Quadrate
Parker, '85 '85a	Incus			Quadrate	Articulareand Angulare
Parker & Bettany, 77		Incus	Otic capsule	Hyomandibula	
Peters, 67	Tympanic		Columella	Extracolumella	Extracolumella
Platner, 39	Glenoid reg'n				
Rabl, 87			Hyoid arch	Mandibular arch	Mandibular arch
Reichert, 37	Incus		Hyoid arch	Quadrate*	Prox. end Meckel's
" 38a	Incus	Stapes	Hyomandibula-columella	Quadrate	Prox. end Meckel's
Reynolds, 97	Tympanic ring		Columella		Extracolumella
Salensky, 79,80			Periarterial	Prox end Meckel's	Prox. end Meckel's
Schenck, 74			Hyoid	Meckel's cartilage	Meckel's cartilage
Schäfer, 94, 96			Hyoid	Meckel's cartilage	Meckel's cartilage
Schultze, 97	Incus		Otic capsule plus hyoid	Palato quadrate	Meckel's cartilage
Staderini, 91					
Wiedersheim, 82	Incus		Otic capsule	Quadrate	Articulare
" 86	Malleus and incus			Quadrate	Articulare
" 97	Incus	Stapes	Hyomandibula	Quadrate	Articulare
" 98					
Zittell, 89, p. 444			Meckel's cartilage		
" 92	Incus		Hyoid	Quadrate	Articulare
Zondek, 95			Hyoid	Mandibular arch	Mandibular arch

*Reichert describes mandibular arch as consisting of three parts, the upper being the pterygoquadrate, the lower Meckel's cartilage; hence the middle must be the quadrate although not so designated by him.

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To the above we must add the words with which Versluys ends his admirable memoir ('98) "Wir kommen also zu dem Schluss, dass die Gadow'sche Deutung der Homologie der Gehörknöchelchen mindestens eben so gut wie die Reichert'sche die jetzt bekannten Thatsachen mit einander in Einklang bringt." Yet on p. 220 he says that incus and malleus are derived from the posterior prolongation of Meckel's cartilage and hence must be homologues of the quadrate and articulare.

An analysis of the above table shows that, as a rule, the osteologists and paleontologists are in general agreement in the view that the quadrate is not an element of the mammalian chain; while almost as universally those who have approached the problems from the developmental standpoint recognize in either incus or malleus the quadrate. The first group base their conclusions solely upon adult skeletal structures with but little reference to other parts except ligamental connections, while not infrequently the possession of processes by the extracolumella is adduced as evidence placing the homology of this portion with both incus and malleus beyond a doubt.

The fate of the mammalian quadrate is explained in two ways. According to the one it has been absorbed in the glenoid region or the zygomatic process and this absorption or fusion is assumed as proved, regardless of the fact that the quadrate, in all places where it indisputably occurs, is a cartilage bone, while so far as is known no cartilage ever appears in the zygomatic region. The embryologists apparently are nearer the solution, but in their papers there is little attention paid to the results of the osteologists. In my opinion the greatest contribution of Dr. Ruddick and myself to the whole question is that we pointed out that in the auditory chains two entirely distinct elements occur: (1) Those that belong morphologically in front of the spiracle (Eustachian tube), and (2) those which arise behind this landmark. Evidence based upon such premises is clearly of more importance than that derived from ligamental connections or development of processes.

A word may be said here as to the terminology used for the

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sauropsidan ear bones. As is well known they have a shaft-like structure, sometimes continuous, sometimes consisting of two parts, and with various processes developed upon the distal part. To this whole structure the term columella was given at first. Later great diversity has been introduced, some have called the end inserted in the fenestra ovalis, the stapes; the shaft, columella; and the distal parts by a multitude of names—extra-columella, epistapedial, suprastapedial, etc., while still others, like Dollo and Peters, influenced by their views of homology, have called these distal portions malleus, incus, etc. Here the term columella is used as implying the whole sound-conducting apparatus, and, as will be explained later, this columella is regarded as being composed of two parts, a proximal stapes and a distal extracolumella, this latter term being adopted from the pages of Versluys ('98.)

MATERIAL AND METHODS.

In my studies I have investigated with more or less detail embryos of Amblystoma, Amphiuma, Ichthyophis, Pipa, Sceleporus, Alligator, and the pig. These studies have been chiefly made by means of serial sections, although dissections of the larger embryos have been made. Wax reconstructions after Born's method have been made of almost every stage studied so far as the skeletal elements were concerned. The course of the nerves has been worked into these models from drawings made by projection from the sections. Sagittal sections have proved the most instructive, but these have in most cases been compared with sections cut in other planes.

THE MIDDLE EAR OF THE URODELES.

The relations of the bones in the middle ear region of the urodeles have been investigated by several students, the most prominent of recent writers being Hasse, '73; Huxley, '74; Parker, '77 and '81; Wiedersheim, '77 and '80; Stöhr, '79; Cope, '89; Hay, '90; Kingsley, '92; Platt, '97 and Winslow, '98. In the urodeles, as was stated above, there is no formation of a tym-

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panic cavity and hence there is no marked development of a chain of auditory ossicles. The outer wall of the otic capsule contains a large fenestra ovalis in which is situated a flattened stapes. Concerning this there are three views. According to Stöhr ('79), and Wiedersheim ('77), it is cut off from the cartilage of the anterior wall of the fenestra by resorption. A second view is that it has arisen by chondrification in the fenestral membrane, while the third is that it has arisen independently of the otic capsule and apart from the fenestral membrane. Parker's ideas ('82 etc.), are a combination of the first and third for he regards it as 'hyotic,' a part arising from the otic capsule and part from the hyoid. The third view commends itself to me, for like Miss Platt ('97), and Winslow ('98), I have satisfied myself that, at least in Amblystoma, the stapes has no connection with the otic capsule or fenestral membrane. I have, however, not been able to connect it with the hyoid at any stage. In this I am in full accord with Reichert ('38), Wiedersheim ('77), Parker ('77), Stöhr ('79 and '81), Hay ('90), Villy ('90), Gaupp ('93), and Winslow ('98), who fail to find such connection in the amphibia. Upon this point, however, see the account of the stapes in the pig.

Several recent writers, Wiedersheim ('77), Gaupp ('93), and Platt ('97), have retained the early name of operculare for the amphibian stapes because of the "questionable homology with the stapes of higher vertebrates." The term is particularly unfortunate since it is easily confused with the gill cover of the teleostomes and also with a bone in the sauropsidan lower jaw; and besides, as I hope to show later, the stapes is probably homologous throughout the whole series of pulmonate vertebrates. It is at least certain, despite the doubts of Miss Platt ('97, p. 431), that the stapes is homologous throughout the small group of urodeles.

In Amblystoma and several other urodeles (Winslow), the stapes is without direct articulation with any other skeletal element, although (cf. Wiedersheim '77), it usually has a ligamental connection with the quadrate. In a second considerable series

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—Necturus,* Ellipsoglossa, Cryptobranchus, Menopoma (Wiedersheim '77), Sieboldia (Parker '82), Plethodon (Winslow '97), and Amphiuma,—the stapes enters into direct articulation with the quadrate by the intervention of a 'stapedial' process developed from the quadrate. Exactly the same relations occur in the Gymnophiona (Wiedersheim '79, the Sarasins '90, Cope '89, Winslow).

The ligamental connection of stapes and quadrate referred to in the preceding paragraph is utilized by Iwanzoff ('94) to prove that there is an extracolumella in the urodeles. I do not understand him in all points, but he seems to regard the stapes (operculum) of siredon as described by Wiedersheim and Parker as forming a part of the extracolumella, the remainder being formed by the stapedio-quadrate ligament while a "round cartilage on the hinder wall of the skull" is considered the true stapes, since the levator scapulæ muscle is attached to it, while in Rana the same muscle is attached to the stapes proper. If muscular attachments are to decide stapedial homologies things are in a bad way, for according to Iwanzoff's own showing this same muscle in the reptiles is attached to the transverse process of the first vertebra and reaches no farther forward.

The principal points regarding the urodeles and cæcilians which I wish to make are that the stapes may articulate directly with the quadrate, and since this element in turn articulates with the articulare, we have here a chain of bones connecting the fenestra ovalis with the lower jaw. A second point is that it is probable that, since this feature is common to both urodeles and gymnophiones, it has probably been derived from some common ancestor, for there remains now no evidence (see Kingsley '92) that the cæcilians have descended from Amphiuma-like forms;† but rather the whole cranial structure proclaims them

*Cope ('89), says that in Necturus the articulation is with the squamosal (paraquadrate); my preparations show that a cartilaginous portion intervenes and that the articulation is with the quadrate.

†Davison ('95, '96), has described what he regarded as a tentacular apparatus in Amphiuma. I have examined his sections, which he kindly sent me, and find that his tentacle was in reality a trematode parasite lying in the blood vessel running beneath the eye.

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an ancient type, a view which receives farther confirmation from their wide and discontinuous distribution, although as yet no fossils have been formed in any formation.

THE MIDDLE EAR OF THE ANURA.

For our knowledge of the development and relations of the structures of the middle ear in the anura we are largely indebted to the accounts of Parker ('71), Parker and Bettany ('77), Villey ('90), Marshall ('93) and especially to Gaupp ('93 and '96), while certain details are furnished by Rathke ('32), Duges ('35), Reichert ('38), Stöhr ('81), and Cope ('85,'89). It is greatly to be regretted that the accounts furnished by these writers are deficient in certain features where we could wish more detail, but the investigation is involved in great difficulty on account of the great changes introduced at the time of metamorphosis which render the tracing of parts a more or less uncertain matter.

In the frog (Gaupp) a large fenestra ovalis occurs, and in the posterior part of this a large stapes arises by autogenous chondrification. In front of this a separate chondrification occurs in the proximal end of a strand of tissue which extends from the fenestra to the quadrate. Until after metamorphosis this bit of cartilage, (pseudoperculum, Gaupp) which forms the proximal end of the extracolumella, remains small. With the shifting of the parts at the time of metamorphosis the quadrate moves back into the region of the ear and there develops a posterior part, the tympanic annulus, and an anterior portion, the definitive quadrate of the adult, with suspensorial functions. The distal end of the extracolumella now arises in connection with the tympanic membrane and joins the pseudoperculum; stapes, pseudoperculum* and distal portion constituting the columella of the adult. As the shifting continues the

*One is tempted to suggest that this psuedoperculum, arising as it does as a distinct element, may be the symplectic of the fishes. This is the more reasonable if we regard the stapes as hyomandibular, and suppose, as seems probable, that the amphibia have descended from a crossopterygian rather than from a dipnoan ancestry.

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quadrate finally comes to lie behind the tympanic annulus, but both of these parts are in front of the tympanic cavity and Eustachian tube, while stapes and pseudoperculum are behind the same cavity.

The figure of the otic region of Pipa after the metamorphosis (fig. 1) illustrates well the resulting conditions. The fenestra ovalis is nearly filled by the elongate plate-like stapes which connects in front with a similarly shaped pseudoperculum. The distal element, the extracolumella, has fused with the pseudoperculum, and except for a slight notch, my specimen affords no evidence of its originally distinct character. I am, however, willing to accept the account of Gaupp (93 p. 393) of its independent origin; see also Cope ('89). The columella, formed of these three elements—stapes, pseudoperculum and extracolumella—projects forward, outward and slightly downward, the pseudopercular portion lying in the posterior wall of the tympanic cavity, the extracolumella extending forward, parallel to the axis of the body, into the tympanic membrane. The anterior and ventral walls of the tympanic cavity are supported by the nearly semicircular annulus tympanicus.

The quadrate, in its backward migration, has come to lie with its body behind the tympanic annulus but it sends processes forward which are continuous with the pterygoid and trabecular tracts of the chondrocranium as has been described by Winslow ('98) in this genus and by Stöhr, Parker, Gaupp and others in other anura. Posteriorly the body of the quadrate is distinct from the otic capsule although closely applied to it. From this description it will be seen that here as in urodeles the quadrate is fixed and incapable of motion—to use the terms of Stannius, it is streptostylic.

As a whole the anura throw but little light upon the ossicula auditus in other forms. In one point they are interesting in that they show the existence of a distinct element in the columella between the stapes and the extracolumella, an element of which I have seen no evidence in any other group. Again the formation of a tympanic annulus is suggestive in connection with the os tympanicus of the mammalia.

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THE MIDDLE EAR OF THE LIZARD.

The lizard embryos, which form the basis of the following descriptions, were not identified beyond a doubt. They were obtained from the Brimleys, dealers, at Raleigh, N. C., and were sent by them as belonging either to *Sceleporus undulatus* or *Cnemidophorus sexlineatus*. They were too large for Oligosoma or Eumeces. Some of the embryos were so far developed as to show clearly the characters of Sceleporus, and it is possible that all may have belonged to that form. In the stages sectioned there were no features recognized which would lead me to suppose that I was dealing with two distinct forms. Still, on account of the uncertainty of identification, I speak of them as lizards, without farther attempt at indication of genus or family. In the descriptions which follow no attempt has been made to indicate age, since no published figures are at hand for comparison, and measurements could not be made, since the embryos were coiled and hardened in that condition.

In the earliest stage studied the various elements of the visceral skeleton were in the procartilage stage, and even in Meckel's cartilage—the first to show the formation of true cartilage —there was no formation of interstitial substance, the tissue being indicated merely by the more crowded condition of the nuclei.

In this stage (figs. 2, 3, 15,) the pterygomandibular arch forms a continuous stroma, without trace of division into the elements —pterygoid, quadrate and Meckel's cartilage, which are later differentiated in it. The quadrate region, however, is recognizable on account of its greater size. From it the pterygoid extends forward and inward, as a slender rod, towards the trabecular region, but with, at this stage, no connection with any other cranial structure. The Meckelian is also slender, but calls for no remark.

The pharyngeal region is a broad, flattened tube, with two broad diverticula on either side, which are distinct from each other only in the distal portion. The anterior diverticulum,

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which gives rise to tympanic cavity and Eustachian tube, is dilated distally in a vertical direction, and it is this distal dilatation which forms the cavity of the middle ear. The quadrate portion of the mandibular arch lies just in front of this tympanic portion and below the side of the pharynx.

The hyoid arch is united below by a continuous stroma (basihyal) with its fellow of the opposite side, and also with two branchial arches (I and II). Of these latter the first extends upwards nearly to the cranial wall, while the other is composed of a ventral portion (hypobranchial), and separated from it by a considerable interval a more dorsal part—possibly epibranchial. Between these two no trace of intermediate parts occur. These branchial arches have no relation to the otic elements, but are mentioned here as showing the features already characteristic of the adult (*cf.* Cope, '92, pl. IV., fig. 14), except that the epibranchial of the second arch has not been recognized in mature animals.

The hyoid extends upwards and outwards to a point just behind the tympanic wall, and there comes into very close connection with the distal extremity of the stapes. Between these two elements the procartilage tissue is little less dense than at other points, but I have no doubt of the original continuity of the two. Later, as we shall see, the hyoid loses all connection with the stapes, and the break existing at present is possibly the beginning of the wider separation which occurs later.

The stapedial portion of the stroma runs inward from its point of connection with the hyoid proper and at an angle of about seventy degrees with it. Its proximal end terminates a short distance from the labyrinth of the inner ear, its shaft lying above the lateral portion of the pharynx. Proximally it has no connection with the otic capsule, which is just beginning to be differentiated, while the stapedial tissue is much more dense.

Another element enters into the composition of the columella —the extracolumella—and my studies show that at first this is a discrete part. It appears at first as a slender rod of procartilage just in front of the hyoid and ventral to the tympanic

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cavity. Its upper end is closely related to the dorsal end of the hyoid and the distal end of the stapes (figs. 2 and 3), but ventrally it runs down into the undifferentiated tissue, which is later to form the tympanic membrane, extending into close connection with the ectoderm. At this lower end its relations are of considerable interest (fig. 15). As shown in this parasagittal section, a groove appears just in front of this extracolumella, and a second and deeper one behind it. The anterior of these lies in the line between extracolumella and the outer edge of the quadrate, while the second and deeper one, if continued, would cut between hyoid and extracolumella. The second of these clefts, if traced dorsally, is seen to be the ventral part of the groove, which more dorsally forms the external meatus. In other sections a similar groove occurs between hyoid and the first branchial. From reasons of relation, as well as from other facts to be detailed later, I am strongly inclined to regard these grooves as remnants of visceral clefts; and if this be true, there is a cleft indicated between the external meatus and the first branchial. In other words I see here two clefts between the quadrate and the hyoid.

This stage of the lizard, to summarize, shows that the stapes is derived from the hyoid arch, and that the otic capsule, at least at first, contributes nothing to it. The stapes is post tympanic in position, but the evidence afforded by this stage is not sufficient to decide whether it is to be regarded as a hyomandibular or not. Evidence from other forms which would render such an homology probable will be discussed later. The recognition of the extracolumella as an independent element has not been made before. I believe it to be the remnant of a former gill arch. A discussion of the reasons supporting this view will be given farther on.

In later stages of the lizard the features already described can be made out with certain modifications. It is not necessary to follow through the various stages in detail, but merely to describe the changes introduced with growth. With the formation of cartilage, pterygoid, quadrate and Meckel's cartilage become

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differentiated, the quadrate extending upward and backward, above the tympanic cavity, to articulate with a process developed from the upper posterior wall of the otic capsule, which is now chondrified. With the chondrification of the otic capsule the fenestra ovalis is formed, which is nearly filled by the proximal end of the stapes. The hyoid loses its connection with the stapes, and all traces of the strand of procartilage which made the connection in the earlier stage disappear.

Stapes and extracolumella are indistinguishably fused into the well-known columella, the distal end of which becomes expanded into an irregular plate, from the anterior ventral angle of which is given off a process which extends into the tympanic membrane (figs. 10 and 12). The other skeletal parts call for no special mention.

The question naturally arises as to how much of the columella is stapedial and how much extracolumellar in origin. At this stage there is no means of saying, but the studies of various authors, and especially of Versluys upon the adult, give some hints. In various genera the columella is composed of two parts, articulated on each other, but in other forms, while no moveable articulation occurs, the proximal part of the columella is cartilaginous, while the outer is ossified. These facts lend some support to the view that the columella is a compound structure, the line of demarcation of its two elements occurring near the middle of the shaft. At this point of junction in several species there is a downward projection, the processus internus of Versluys, from which a ligament proceeds to the inner surface of the quadrate. Peters thinks that he has been able to trace this ligament into the lower jaw, but, studying the same species, Versluys is not able to confirm him on this point. Versluys is strongly inclined to regard the descending process as belonging to the extracolumellar part of the columella. Hence, as we find in later stages a processus internus developed at about the junction of the middle and outer thirds of the columella in the form here described, it would appear probable that the definitive columella is about one-third extracolumella and two-

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thirds stapedial in origin. It is, however, probably that in some cases (e. g. Sphenodon) the columella is almost wholly stapedial, the extracolumella being reduced to an inconsiderable element.

At first, as we have seen, the columella lies at first outside of and behind the tympanic cavity. With growth it invades the cavity, or rather, the cavity grows backward above and below the columella, thus enclosing this element in a fold of membrane so that it apparently extends through the cavity while the true relations are shown by the connecting band (fig. 17).

Another point must be mentioned. The facialis nerve, upon leaving the skull, courses backwards around the outer wall of the otic capsule, passing above the columella. After passing the columella it gives off the chorda tympani nerve which passes forward, also above the columella, to enter the lower jaw. From this it appears that the columella lies between the two main divisions—hyomandibular and chorda tympani—of the facial nerve and is posterior to the latter ramus, a point which is of some value in comparison with the mammals. (Figs 10 and 14.)

In embryos just before the migration of the columella into the tympanic cavity the Eustachian tube is much narrowed from its more primitive condition and is seen to divide distally into two parts (fig. 13) one of which extends outward between quadrate and columella, while the other extends backward behind the columella. From these two outgrowths the tympanic cavity is formed and comparison with earlier stages leads me to think that these represent at least two distinct gill clefts, the anterior being equivalent to the spiracular of the elasmobranchs, the posterior being the first branchial. Comparison with the rudimentary clefts described on the external surface would lead one to regard the outgrowth between columella and quadrate as double in character, but in none of my sections have I seen any evidence of this.

The same figure (fig. 13) illustrates another point which occurs in several species of lizards according to the investigations of Versluys. This is a ligamental connection between the pro-

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cessus internus, developed on the lower anterior surface of the columella, and the upper inner surface of the quadrate. This at once suggests comparisons with the conditions occurring in the caducibranch urodeles, the discussion of which will be taken up in the second part of this paper.

THE MIDDLE EAR OF THE ALLIGATOR.

The alligator must have an important place in all discussions of the homologies of the ear bones and especially so since Peters relies largely upon this form to establish his points. For the material used I am indebted to Professor Samuel F. Clarke of Williams College, who kindly allowed me to study two stages from his valuable series of this animal. While the lizards belong to the strepostylic reptiles, the alligators are monimostylic i. e., in the adult they have immovable quadrates.

In the stage figured, which corresponds closely to Clarke's ('92) fig. 45, of a lizard embryo, the general relationships are much as in the description of Peters ('68*), Huxley, and Gadow, in their studies of much larger animals. The Meckelian is a long slender rod, slightly enlarged at its proximal end where it articulates with the quadrate. The quadrate itself (fig. 16) is very large and massive and gives off from its antero-internal surface a slender pterygoid bar. Its posterior surface is excavated on the outer side where it abuts against the anterior wall of the tympanum, and the dorsal portion projects distally beyond this excavation as a slender crest. Its upper portion is enlarged for articulation with the ventral surface of the otic region of the chondrocranium above the fenestra ovalis. A point of no little importance is that at this time the quadrate is freely moveable. It only becomes firmly fixed (streptostylic) with the development of the paraquadrate which unites it to the cranium.

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*Huxley has pointed out that Peters made a most serious error in his identification of parts in the alligator, but these corrections have been utterly ignored by those (Baur, Cope, etc.,) who have claimed that Peters had settled the question of the homologies of the ear bones. In saying that my results agree closely with the account of Peters I am to be understood as implying that the corrections pointed out by Huxley have been made.

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The fenestra ovalis is key-hole-shaped, the broader end being uppermost; the lower anterior part is almost completely filled by the somewhat expanded basilar portion of the stapes. From this basilar portion the columella extends outwards and downwards behind the tympanic cavity. At about its middle part it gives off a processus internus, directed upwards and outwards, and this approaches very close to the upper part of the quadrate, but does not articulate with it. At this time there are no traces of a ligamental connection between this processus internus and the quadrate, but the relations are significant when viewed in the light of ligamental connections which exist in many lacertilians. Distal to this processus internus the columella becomes expanded into a larger extracolumella.* Viewed from the side this extracolumella is somewhat triangular in outline and from the hinder angle a cord of cartilage—already described by all who have studied this region in any of the crocodilia—passes backwards and then downwards around the inferior posterior angle of the quadrate, and connects with the proximal end of the Meckelian, just behind the quadrato-Meckelian articulation. This columella-Meckelian cartilage is much smaller in diameter than Meckel's cartilage. I have no evidence as to its origin in the alligator, but from conditions occurring in other forms I consider it to be formed *in situ*, and to be exactly equivalent to the similar band in the mammals which forms the collum of the malleus, connecting the body of the malleus with the manubrium. I cannot subscribe to the suggestion of Peters ('68) that it may represent the incus or orbiculare of the mammals, nor the view of Huxley ('69) that it is the stylohyoid. Parker ('83) regards this connection as composed of epi- and ceratohyal but he offers nothing worthy of the name of proof to support such an interpretation. My preparations show no such distinct elements as he figures, the cord being continuous throughout. This connection between Meckel's cartilage and the extracolumella, like that between the extracolumella and the hyoid arch, is

*My sections at this stage show no break in continuity between stapedial and extracolumella.

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rather to be compared with the connections which form in various ichthyopsida between the proximal ends of the branchial arches. As Gadow points out, it has nothing to do with the siphoneum. Gadow's suggestion that the system of cartilages and ligaments extending from the fenestra ovalis to the mandible is at least analogous with . . . . . the hyomandibulo-symplectic element of the fishes, hardly applies here, for the piscine chain of elements includes the quadrate as one constituent. In the crocodilia the quadrate is outside of this system.

THE MIDDLE EAR OF THE PIG.

In pig embryos 15.5mm. long no cartilage has as yet been formed, but procartilage is forming, and tracts of this stand out plainly in the stained section on account of the crowded condition of the nuclei (fig 7). In modelling this and similar early stages there is difficulty in saying just where procartilage leaves off and undifferentiated tissue begins, since these fade into each other and there is not that sharp differentiation which occurs later, when cartilage and perichondrium are formed. I have, however, modelled two embryos of this stage, one from transverse and the other from sagittal sections, and finding them to agree closely conclude that there is no serious error in them.

At this stage there is not the slightest indication of an otic capsule, the membranous labyrinth being surrounded by undifferentiated mesenchyme, in which the nuclei are as scattered as at any other place. The tracts of procartilage (fig. 6) represent the incudo-Meckelian, manubrial and hyostapedial tracts, each of which is formed of a continuous stroma and separated from the others by regions of undifferentiated mesenchyme. Meckel's cartilage extends distally as a recognizable structure into the lower jaw to a point about midway between the angle of the mouth and the tip of the jaw. The cartilages of the two sides are widely separate. Proximally the anlage continues outwards and backwards to a point about on a level with the distal end of the Eustachian-tympanic cleft. It forms throughout a continuous stroma, the distal part of which, destined to become

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the incus, is enlarged and separated from the rest by a slight constriction. Even at this stage it shows traces (omitted in the figure) of the processus longus for articulation later with the stapes, which is as yet remote from it. This part is shown by a slight crowding of the nuclei in the region between the two.

The hyostapedial also forms a continuous tract, sharply bent upon itself (fig. 6a) the proximal or stapedial portion running inward in a nearly horizontal position, while the hyoidal portion occupies its definitive position. The stapedial portion is perforated in its base for the passage of the stapedial artery. As this stapedial portion is also curved on itself it frequently appears as if it arose, as claimed by Salensky and others, around the artery without connection with any other skeletal element, but study of serial sections at this stage plainly shows it connected with the hyoid as described here.

Between hyostapedial and incudo-Meckelian tracts is a third element, not previously recognized as distinct in origin from the other parts. This is the anlage of the manubrium of the malleus. It lies nearer the hyoid than to the Meckelian, but on the side towards the hyoid it is sharply marked off from the surrounding mesenchyme (fig. 7) while on the anterior face it gradually fades into the undifferentiated tissue, and there is nothing as yet to indicate the future connection with Meckel's cartilage. As shown by figure 6 it is elongate, with its major axis parallel to the hyoid, but in the model the anterior margin is more definite than it should be. It lies in the tissue just outside of and below the outer end of the tympanic cavity.

The facial nerve at this stage shows many of the relations characteristic of the adult. The main trunk passes backward, running above the stapes in its course. It then bends downward and then runs along the posterior surface of the hyoid. At the most posterior point of its excursion it gives off the chorda tympani nerve which crosses the external surface of the hyoid, then passes forward below the external end of the tympanic cavity, *i. e.* through the tissue from which the tympanic membrane will be developed later, and reaches the upper,

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inner end of the incudo-Meckelian cartilage, where it runs forward in close association with the inferior dental branch of the trigeminal.

In pigs 18mm. long the otic capsule is just beginning to be differentiated, while in the visceral arches the boundaries between procartilage and the surrounding tissue are more sharply marked than before. The incudo-Meckelian tract has extended itself into a closer relationship with the stapes (fig. 9) and its proximal end has begun differentiation into the incus in which we can already recognize a processus longus (stapedial process) for articulation with the stapes, and an anterior process which extends outwards and forwards above the proximal end of Meckel's cartilage, and which eventually forms the dorsal boundary of the articular facet by which the incus articulates with the malleus.

In the hyostapedial arch there is also a differentiation into hyoid and stapes, but as yet the head of the stapes inclines toward the proximal end of the hyoid, thus showing traces of the connection which existed between the two in the earlier (15.5mm.) stage. The stapes itself has its proximal side less prominent than formerly, and is gradually assuming the condition with a flattened basilar plate characteristic of the adult. My sections fail to show the existence of a basilar plate distinct from the rest of the stapes, but the definitive condition of the adult is clearly derived from that of the earlier stage by growth of the proximal end of the hyostapedial. Between hyoid and stapedial the tissue still remains more dense than at other points, but the differentiation between the two has progressed so far that we may speak of them as distinct parts. The hyoid itself calls for no special remark as it plays no further part in connection with the auditory ossicles.

The manubrial cartilage has shown but few changes. It is now somewhat broader, but there is the same difficulty of ascertaining its anterior border that existed before. It still remains much nearer the hyoid than to Meckel's cartilage, but between it and the latter the nuclei are becoming more numerous

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and are beginning to arrange themselves to form the bar of cartilage which extends between the extremities of the tympanic cavity and the external auditory meatus (*i. e.*, in the future tympanic membrane) to connect it with the upper end of Meckel's cartilage, that is, with the future body of the malleus. Apparently Frazer ('82) has seen the beginning of this process without recognition of the manubrial element, for he says that the manubrium develops later than the rest of the malleus. This is true so far as this intermediate band of cartilage is concerned, but not for the distal part of the manubrium.

In the pig, 20mm. long, the otic capsule is well chondrified; the fenestra ovalis is elongate in the direction of the axis of the body and is broadly overhung by the upper part of the wall of the labyrinth (figs. 14 and 18).

The stapes and hyoid are no longer in connection. The hyoid, which now consists of cartilage throughout, has not reached its definitive condition and the connection between its proximal end and the skull has yet to be formed. The stapes has assumed nearly the adult condition and articulates with the incus but its basal plate is not so broad as in the adult, its crura are subequal and there is as yet no prominent capitulum.

The incus has increased considerably in size. The stapedial process is small and short with a distal articular surface. From the upper posterior angle of the body a long slender process extends upwards and backwards and lies along the lateral wall, thus strongly suggesting the condition and shape of the quadrate in the lizard (compare figs. 10 and 14) and lending much support to the view that the incus has, at some time in its history, possessed suspensorial functions. The ventral surface of the incus bears an elongate ridge, running obliquely inwards and backwards, and is convex on its lower surface for articulation with the upper end of Meckel's cartilage.

The manubrial element is still nearer the hyoid than to the Meckelian. It is somewhat more elongate than at first, and now lies in a nearly horizontal position in the tympanic membrane, which, as is well known, is very oblique at first, owing to

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the fact that it is developed by the inpushing of the external meatus beneath the outer end of the tympanic cavity. At the anterior outer side a cartilaginous bar has developed in the stroma between the manubrial element and the Meckelian, connecting the two. This bar and the manubrial element form the manubrium mallei of the adult, the collum arising from part of the connecting bar.

The proximal end of Meckel's cartilage is somewhat enlarged and its dorsal surface bears a shallow groove for articulation with the ridge described on the incus. This rounded incudal surface and concave facet on the Meckelian strongly recall the relations existing between the quadrate and the articulare in the non-mammalian groups. From the enlarged proximal end (caput) of the Meckelian the rest of this arch extends, as a slender rod, downwards and forwards into the lower jaw.

Ossification (of membrane bone) is already in progress in the lower jaw, but the cartilages consumed in the formation of the condylar process has not yet appeared. I may say that these cartilages which have been noticed by several writers have yet to be studied by modern methods and in the light of comparative morphology, for as yet we are without explanation as to their formation and ancestry. I have some facts concerning them, but will leave them for a later time.

In pigs larger than the one last described, up to specimens about 80mm. in length the conditions do not change much from those already described. In the latest of these the connection between the malleus and the rest of the Meckelian persists and ossification has not begun in any of the auditory ossicles. With increase of size the relative prominence of the upper posterior process of the incus is lost and it gradually assumes the shape of the processus longus of that element.

There is, however, one feature in the older specimens that seems to demand notice. Kölliker pointed out (79) that the processus longus bears on its lower surface a distinct membrane bone. In the edentates and marsupials Parker (81) has described the same bone and he calls it the angulare. I find the

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same element in the pig (figs. 4 and 5). It here forms a thin splint of bone lying on the lower and inner surfaces of the Meckelian, behind and distinct from the dentary. I have not ascertained whether the whole of the processus gracilis of the malleus is formed from this element or whether later there is an ossification of Meckel's cartilage in this region. It is certain that in its topographical relations this splint of bone agrees with the angulare of the non-mammalian forms, and such I prefer to call it until this position be shown to be untenable.

GENERAL CONSIDERATIONS.

The matters now coming up for discussion relate to the bearings of the observations recorded in the preceding pages. First of these is the question; is the columella of the sauropsida homologous with the chain of bones in the mammalian ear? or, if not, to what extent can we trace homologies between the two? As will be remembered, Peters, Dollo, Baur, Cope, Gadow and others have sought to recognize all parts of the mammalian chain in the columella, and their accounts are in some cases difficult to understand in details from the fact that they have called parts and processes of the reptilian ear bones by the names malleus, manubrium, incus, etc., derived from the mammalian ear.

To my mind the points brought out by Dr. Ruddick and myself show that this position is perfectly untenable and that this complete homology cannot exist. We showed that the columella first forms in the posterior wall of the tympanic cavity, and is above and behind the cavity itself. Only later does it attain its definitive position as a skeletal rod apparently passing through the cavity by a relative change of parts, the posterior wall pushing back so as to envelope the columella. The stapedio-incudo-mallear chain of the mammals, on the other hand, arises in front of the tympanic cavity, and only later does it enter the cavity from in front in a similar manner during growth.

The relations of these ossicles to the nerves is also instructive. Thus the columella is embraced between the forks of the facialis, the hyomandibular passing behind, the chorda tympani

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in front of it. In the mammals the ossicular chain has no such relationship, both hyomandibular and chorda tympani passing behind it. In other words the columella is behind the chorda tympani, the mammalian bones in front of it.

When we reflect that viseral clefts and cranial nerves are older structures than cartilage and bone, and that skeletal structures are developed in certain relations to these, I think it must be admitted that the sound conducting apparatus in sauropsida and mammals cannot be homologised as a whole. Ligamehtal connections, relations of muscles and peculiarities of shape cannot outweigh such facts as these—cannot permit us to compare posttrematic with pretrematic structures.

If, however, we cannot homologise the ossicular chains in their entirety, it is possible that certain parts may be homologous in each. The evidences for such homologies must be sought in development, relations, etc., taking up each element by itself.

THE STAPES.

The term stapes is applied to that auditory ossicle which is situated in the fenestra ovalis, and is the proximal element in the auditory chain in amphibia, reptiles, birds and mammals. Doubts have been thrown upon its homology throughout this series, and certain writers have called it the operculum in the amphibia because of this very doubt. Various views have been held as to its origin, as may be seen from the tables on pp. 206, 207. It is the hyomandibular, it is developed from the hyoid arch, it arises from the mandibular arch, it is cut off from the otic capsule, it is formed from an independent centre in the membrane of the fenestra ovalis, it is formed around the stapedial artery, it is and it is not homologous throughout the air breathing vertebrates. Pollard ('91 and '92) suggests that it arises either from the first suprapharyngobranchial or as a modification of the otic capsule, where this touches it, in much the same way as the ectethmoid is formed farther forward. The extreme of scepticism as to its identity is furnished by Iwanzoff ('94), who argues that since in certain amphibia the protrahens scap-

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ulæ (levator scapulæ) muscle is attached to the stapes, while in others it is attached to the otic capsule, that even in this group the stapes is not homologous in all individuals. If muscular attachment is to settle stapedial homologies then we must regard the part to which this muscle is attached as stapedial, so that in the reptiles where its insertion is upon the first vertebra we must look in that region for the stapes.

In the lizard and the pig which I studied the stapes develops from the proximal end of the hyoid arch, or at least from the same continuous stroma. This same condition exists in Lacerta (Hoffmann '89) Tropidonotus (Parker '78, Rathke '39) chick (Reichert '37) Columba (Peters '68). Salensky ('79, '80) and Fraser ('82) failed to find it in mammals, but it was seen by Rabl ('87), who shows that it occurs only in the embryo before the formation of cartilage. It therefore appears to be pretty well settled that in sauropsida and mammals a part at least of the stapes is developed from the hyoid arch.

The case of Sphenodon as given by all who have studied it (Huxley, Günther, Baur, Gadow, Iwanzoff, Osawa, Versluys), possesses especial interest in this connection. In the adult of this form the hyoid retains its connection with the columella throughout life, joining with its distal extremity. Versluys has discussed this condition as well as that presented by the other forms above as to whether this connection was with the stapes or the extracolumella. He concludes that in all forms except Sphenodon the connection is with the stapedial portion, while in Sphenodon it is with the extra columella, but he regards this latter condition as secondary. This assumption does not seem to me necessary, judging only by the evidence at hand.

At the risk of getting ahead of my story I would say that if we recall the account given of the development of the lizard (pp. 215 and 216) we see that the hyoid is here continuous with the extremity of the stapes and that the extracolumella appears at the junction of the two. We have only to imagine a fusion of extracolumella with hyoid and a persistence of the hyostapedial connection to have the condition permanent in Sphenodon. It

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should be remembered that in Sphenodon the external meatus is lacking and that instead of a tympanic membrane, the tympanic cavity is bounded externally by a thick mass containing muscles, etc., and that as a result of this we might expect a rudimentary condition of the extracolumella. In other words (compare fig. 2), Sphenodon presents a condition closely similar to that of the embryonic lizard. However, observations on the development of the ear of this form, which I understand are now being carried on, may settle this matter.

A part of the stapes, then, arises from the hyoid; but is it all of such origin? As far as my observations go I have seen no evidence of contributions from any other part in lizard or in pig. Hoffmann however, has a different account ('89) and in this he is confirmed by Gaupp ('98.) He regards the stapes in the reptiles as composed of two parts, an otostapes from the otic capsule and a hyostapes from the hyoid. These two unite and only after their union does the separation between hyoid and stapes take place. In the mammals Hoffmann also argues for a compound stapes, a stapes proper and a capitulum for articulation with the incus. He adduces the additional evidence in favor of this view that the stapedial muscle (which is innervated by the facialis and consequently is to be regarded as belonging to the hyoid arch) is never attached to the body of the stapes but to the capitulum or to the os orbiculare when that is present as a discrete body. Gaupp ('98) has used the chorda tympani nerve as a test of columellar homologies in lizards and frogs, and claims from his observations that the columella is not exactly homologous in the two groups, a new element, the hyostapes being added in the higher group. On the other hand, various writers, Dreyfuss ('93,)Broman ('98,) Staderini ('91,) Siebenmann, etc., like myself have seen no evidence in amniotes of otic elements in the stapes; still this is negative evidence and the observations of such accurate students as Hoffmann and Gaupp, are not lightly to be set aside. So we may conclude that in the amniotes the stapes is derived from the hyoid with possibly additions from the otic capsule.

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Another point of importance in deciding the homologies of the parts called stapes, lies in the fact that in certain forms* it is perforated for the passage of a blood vessel (arteria perforans stapedis). It is true that this artery has different origins in different forms, arising in lizards from the internal and in mammals usually from the external carotid, but as is well known, origin is of much less importance in settling homologies of blood vessels than is distribution (*e. g.*, compare the subclavian arteries of a lizard with those of a bird or mammal) and the distribution of this stapedial artery is much the same in either case. I think we are forced to regard this artery as the same, no matter from which carotid it arises, for otherwise we must imagine that we may have even in the group of mammals two different stapes each perforated by an artery.

I think then, that the stapes, arising at least in part from the hyoid, situated with its base in the fenestra ovalis and perforated by the same blood vessel in different groups, must be regarded as homologous throughout the whole group of amniotes.

In the amphibia we have not so much proof of the nature of the stapes. All students of the development of the skeletal parts in these forms (Reichert, '38; Wiedersheim, '77; Stöhr, '79, '81; Willy, '90; Gaupp, '93; Winslow, Parker, etc.;) fail to find any connection at any stage between hyoid and stapes. Iwanzow, however, finds such a connection in the adult Bombinator. There remain, however, some features which may aid us in settling the matter. There is here much uncertainty as to the origin of the stapes, some regarding it as derived from the otic capsule, some as arising independently. In all cases it is situated in the fenestra ovalis. I think that it requires no argument to prove that it must be the same structure throughout the urodeles. In many urodeles (pp.) the stapes articulates with the quadrate. In the cæcilians exactly the same articulation occurs. Hence it would seem to follow that the stapes must be homologous in urodeles and gymnophiones. In the cæcilians

*Certain geckos, some birds and all mammals.

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—Siphonops (Wiedersheim), Dermophis (Cope), Ichthyophis—the stapes is perforated for the passage of an artery with essentially the same distribution as the stapedial artery of the amniotes. So even if continuity with the hyoid be lacking I think we are justified in the assumption that the stapes is homologous in all air-breathing vertebrates.

It is rather more difficult to decide whether the stapes is the equivalent of the hyomandibular of the fishes. We have seen that in certain amniotes the stapes is developed from the proximal or dorsal part of the hyoid, but this of itself is insufficient to decide the question. The hyomandibula, as will be remembered, arises from the dorsal part of the hyoid arch; it loses its connection with that arch and assumes, either directly or by the intervention of the symplectic, the function of a suspensor of the jaws. In those fishes (teleostomes) where distinct elements are developed in the mandibular arch, this suspensor articulates with the quadrate. Now then consider that in some forms the stapes developes from the hyoid arch; that in many urodeles and cæcilians it articulates with the quadrate as a hyomandibula should, while in many lizards it is connected by ligament with the quadrate, it seems at least probable that we have in the stapes the representative of the hyomandibula, an element which must otherwise be entirely lacking in the air breathing vertebrates. This evidence however, is not conclusive, but is certainly not to be ignored.

The symplectic may be mentioned in this connection. I have no evidence of its reappearance in the higher vertebrates if we except the cases of the pseudoperculum of the anura and the os orbiculare of the mammals. The pseudoperculum has little claim in this connection other than it is an element distal to stapes. The os obiculare, on the other hand, lies, like the symplectic, between the hyomandibula (stapes) and the incus which I hope to demonstrate later is the quadrate of the mammals. I have no evidence on this point other than that furnished by position, and need not discuss it farther.

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THE EXTRACOLUMELLA AND THE MANUBRIUM MALLEI.

The view that the extracolumella arises apart from the stapes, and that the columella is a compound structure, is not new. Almost every student has recognized the fact that in the adult it is composed of two parts, while for some every process given off from it is a separate portion. This has been especially true for those who have sought to recognize all the mammalian ossicles in the columella. But the fact that the portion of the manubrium of the mammalian manubrium arises distinct from the body of the malleus, that it is at first, like the extracolumella, a separate element developing in the tympanic membrane, and only later uniting with the rest of the structure, has not been noticed before. Frazer alone has pointed out that the manubrium arises later than the rest of the malleus.

This fact of identity of place of origin goes far toward supporting the view that extracolumella and the manubrium mallei are homologous, but there are several other facts which add probability to this view. It will be recalled that, as described above, and this is in full accord with all who have studied the crocodilia, that in these forms there is a cartilaginous connection between extracolumella and the Meckelian cartilage, a connection comparable to that which exists between the manubrium and the body of the malleus, and this mallear body is, as will be remembered, the proximal end of Meckel's cartilage. Again, in the young of at least some species of birds (Peters, '69; Gadow, '88. p. 474; Versluys, '98, p. 167), there also exists a similar cartilaginous strand connecting the same parts.

I am strongly inclined to regard this element as the remains of a visceral arch which has almost entirely disappeared from between the hyoid and the mandibular arches. In support of this view we have not only the fact of its intermediate position, but in its earlier stages in both lizards and mammals it has the form of a cartilaginous rod lying parallel to the other visceral arches. Here, too, should be mentioned the peculiar condition presented by the extracolumella of the amphisbænans, where,

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instead of a plate limited in extent by the tympanic membrane, the extracolumella extends downwards and forwards as a slender cartilaginous bar alongside the outer surface of the lower jaw to about its middle point (Versluys), or not quite so far (Peters, '82).

This view of these elements as visceral arches receives strong support from embryology, for there is considerable evidence which goes to show that a segment is in the process of being lost in this very region. The first to suggest this loss of a somite was van Wijhe ('82), who based his opinion upon the head cavities. Thus he says, speaking of the elasmobranche: "Die erste Kiementasche liegt im Stadium J nur mit ihrem vorderen Theile unter dem hinteren Theile des zweiten Somiten; vor ihr befindet sich die Kieferhöhle; sie scheint ungezwungen in das Schema zu passen; nur muss man annehmen, dass sie ein wenig nach hinten gerückt ist, da sie grossentheils unter dem dritten Somit liegt. Letzeres ist ohne zugehörige Kiementasche; um auch für dies Somit das Schema gelten zu lassen, muss man annehmen, dass eine ursprünglich (phylogenetisch) unter seinem hinteren Theile liegende Kiementasche abortirt ist, und dass dem zufolge die Hyoidhöhle zwei Visceralbogenhöhlen repräsentirt; dass also der Hyoidbogen potenziell aus zwei Visceralbogen besteht."

Dohrn ('85), basing his arguments largely upon skeletal structures, concludes that there are *two* segments between the mandibular and hyoid arches, one of these being represented by the cartilage of the spiracle (spiraculare) and the other by the hyomandibular, which he, in contrast to other students, regards as distinct and not as primitively a part or the hyoid arch. It should be recalled in this connection that Miss Platt ('91) claims *two* head cavities between the hyoid and mandibular somites. The hyomandibular, according to Dohrn, developes entirely independently of the hyoid, and it has its own dorsal muscles comparable to those of a true branchial arch. He quotes, in support of his position, the observations of van Wijhe upon nerve relationships in the ganoids and Ceratodus. Gegenbaur ('72) had

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previously regarded the spiraculare as formed by a fusion of the cartilaginous gill rays, but with Dohrn it has an individuality, and he points out that in the true gill arches the rays lie between the artery and the cleft, while the spiraculare is separated from the spiracular cleft by the spiracular artery. Dohrn does not attempt to homologise these elements in the elasmobranchs with those of higher forms, but merely suggests comparisons with the symplectic and quadrate, This view of Dohrn, that two segments intervene between mandibular and hyoid has obtained little acceptance. I recall only the remark of Beard ('85, p. 106), "I agree fully with van Wijhe's view that there are two segments in the hyoid arch, and this apart from the hyomandibular portion."

In this same year (1885) Beard came to similar conclusions regarding the disappearance of a segment in this region. He accepts van Wijhe's conclusions drawn from head cavities, and reinforces them with arguments drawn from the facial nerve. He claims that in the elasmobranch two suprabranchial sense organs are developed in connection with this nerve, one above the spiracular cleft and another at the point of division of the anterior branch of the nerve into ophthalmicus superficialis major and buccalis rami. This anterior sense organ is without a cleft. The nerve itself shows a similar double character, for it presents two 'suprabranchial' nerves (*i. e.*, the ophthalmicus superficialis major and the buccalis). "To my mind the best explanation of these two branches is that the facial is composed of two cranial segmental nerves, and this apart from its fusion with the auditory."

Orr ('87), and following him Maclure ('90), introduced a new element into the discussion of the segments of the head in the neuromeres of the central nervous system. According to these there is a neural segment of the brain between the two neuromeres which give rise to the trigeminal and facial nerves. The observations of Locy ('95, *cf.*, however, Neal), point also in the same direction. Neal ('98), the latest student of this problem, admits a rudimentary segment at the same point. He recog-

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nizes the segmental value of the somites of van Wijhe, and accepts the arguments of that writer. He thinks that the ventral portion of the somite may have fused with that of the mandibular arch, and the nerve with the trigeminal.

On the other hand, Hoffmann ('94) describes a rudimentary nerve developing in Acanthias between the facial and glossopharyngeal; he tries to show that there cannot have been a somite dropped from between the mandible and the hyoid, but that, on the other hand, a pair of gill slits have disappeared between the mandibular arch and the mouth.

Summarizing the foregoing, and setting aside the arguments of Hoffmann against the views of van Wijhe (which to my mind are not conclusive), I think that it is safe to assume, from the evidence of head cavities, nerves, neuromeres, and according to Dohrn, skeletal elements, that a somite has been almost completely lost in this region. This much can be said without coming to a decision as to whether the abducens is the ventral nerve root of this segment, whether its dorsal root has been merged in the facialis (Beard), or in the trigeminal (Neal), or accepting with Dohrn both hyomandibular and spiraculare as segmental in nature. We have here, then, the somite, and this cartilage, so far as a rudimentary structure can, seems to fulfil the conditions required of its branchial arch.

I am not ready to admit that the hyomandibular has the value Dohrn would give it, but the spiraculare seems to have more claims to segmental rank, but I cannot decide at present whether the extracolumella (or manubrium) is homologous with this element. It arises opposite the end of the Eustachian cleft; to correspond with the spiraculare there should be a cleft between it and the hyoid, but I have never seen indisputable evidence that this cleft is double. It is true that at its outer end it divides into two forks, but this forking might be explained by its expansion around the manubrium or columella (see fig. 13.)*

*It is possible that here lies the explanation of a part of the discrepancies existing in the accounts of the development of the tympanum by Hunt ('77), Urbantschitch ('77), Moldenhauer ('77), Mall ('88), and Tuttle ('83).

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I have not met in my sections any trace of an extracolumellar element in the urodeles. Parker and Bettany ('77, p. 135) say that "an ossified (spiracular) leaf behind the operculum occurs in Desmognathus and Spelerpes," but in Parker's complete paper ('79), in which he deals with these genera, no mention is made of this element. It is possible that some of the cartilages described by Wiedersheim ('77) as occurring in front of the basihyal in several urodeles may be remnants of the ventral portions of this intermediate arch.

It may be that the groove alluded to on p. 216 may be an external remnant of the gill cleft, which would, in this case, be between the extracolumella and the mandible, while apparently there the external meatus lies between extracolumella and hyoid. In the mammals, on the other hand, the external meatus lies between manubrium and the mandibular arch. It should not be forgotten that Küpffer (93) has described a possible gill cleft in this region. This question can only be settled when we know whether a gill cleft has been lost between the spiracle and the mouth, or between the spiracle and the first gill cleft of the elasmobranch. Dohrn ('85, p, 10), says, "Aber eimnal ist de angebliche oblitirte Kiementasche noch vorhanden, nur dislocirt," but in reading his paper his explanation of this remark has escaped me. Van Bemmeln ('85), however, describes an anterior extension of the spiracular cleft in elasmobranchs which should be thought of in this connection.

THE INCUS.

The incus arises from the proximal end of the same continuum which more distally gives rise to Meckel's cartilage. At first, contrary to Broman, I find it indistinguishable from the rest of the arch, but even in the later precartilage stage it becomes marked off from the more ventral portion by the development of a constriction. With the appearance of cartilage the line of separation is more marked, for the centre of chondrification is entirely distinct from that of the rest of the arch. At first the incus is plainly without connection with the stapes.

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With the appearance of cartilage the lenticular process for articulation with the stapes is developed and a little later a crest is developed on the external surface which extends dorsally and posteriorly as a strong process to the outer surface of the otic capsule above and behind the fenestra ovalis. In the meantime the surface for articulation with Meckel's cartilage becomes developed and takes a form which calls for special mention. The articular facet of the incus is a ridge running obliquely inwards and forwards and is convex at right angles to its length, while on the proximal portion of the Meckelian there is a corresponding concave groove.

The incus is, according to my belief the quadrate (or at least the greater part of that element, since it is possible that a part of it may be found in the tympanic). This view, first formulated by Reichert, has been pretty generally accepted by embryologists. The argument in its favor are :— (1) Its development from the first visceral arch ; (2) Its position in front of the first visceral cleft (the mouth excepted); (3) Its articulation with the stapes (hyomandibula); (4) Its upward and backward extension towards the upper otic region (similar to that found in the quadrate of lizards); (5) The character of its articulation with the Meckelian. In short were we to study the embryo before the appearance of bone in the skull, every feature of the incus would suggest the quadrate and not a point, except the absence of an anterior pterygoid prolongation, could be advanced against such an intrepretation.

With growth and changes in relative size and with the development of bone the relations of the parts are somewhat changed and the incus loses its function of a suspensor of the lower jaw which acquires a new articulation farther forward. This difficulty of explaining this new articulation is the strongest objection to the incudo-quadrate homology but, as will appear shortly, the same difficulty must be met by all unless, like Albrecht, they are ready to homologise cartilage bones with membrane bones and to ignore all facts of development.

Leaving for the present this matter of the new articulation of

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the lower jaw there remain a number of objections to the homologies here adopted. The argument of Dollo ('83) may serve as the type of several of these. He claims that if we can find a sauropsidan in which all six bones of the lower jaw are present; in which the columella is broken up into elements, one of which has the shape and relations of a malleus, while a true quadrate is also present, such a form will show that the quadrate cannot be one of the ossicles of the mammalian ear for that is already accounted for. Such conditions Dollo finds in several lizards.

A reply has already been given in this article to this line of reasoning but it may be repeated here. The part which he regards as having the relations of a malleus is the tympanic portion of the extracolumella and this is homologous with a part (manubrium) and not to the whole of the malleus, but this homology and the other one of identity of stapes in the two groups cannot introduce the incus, which is pretrematic and in front of the chorda tympani, into the columellar tract, all parts of which are post trematic and lie behind the chorda tympani.

The same facts are also opposed to the conclusions of Frazer ('82), who maintains that the incus is formed from the proximal end of the hyoid "as is shown by the continuity of embryonic cartilage, and its morphological and histological agreement as well as by its relations to the chorda tympani nerve." Not only are the facts quoted in the last paragraph opposed to this view, but there is not that continuity of cartilage in the early stages which he claims, while histological agreement is of no importance. Morphological relations are opposed to this view while there is nothing in the relations of the chorda tympani to the incus which lends support to his thesis.

Huxley has two views regarding the incus. In his first ('64, '67) he accepts the interpretation of Reichert, in the second ('69, '71) he argues that the quadrate is represented by the malleus while he holds that since the incus is related to the stapes and to the walls of the tympanum much as is the columella of the crocodile, and since a small cartilage is developed in the stapedius muscle, it follows that the suprastapedial [a process of the extra

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columella] is the incus and hence cannot be the equivalent of the quadrate. Huxley's observations were made upon animals in which essentially the adult conditions had been attained. Development, however, clearly shows that the incus has not the same primary relationship to the tympanic wall that the columella has. Again the argument that since the incus articulates with the stapes it cannot be the quadrate loses all its force when we recall that in many urodeles a stapedio-quadrate articulation does occur, while hints of a similar previously existing condition in the reptiles are found in the frequently occurring ligamental connection between columella and quadrate.

Again it has been advanced against the homology advocated here that incus and Meckelian do not arise separately but are formed from a continuous stroma and hence must be regarded as parts of one continuum, that of the lower jaw. This, however, is not an argument of real importance, for we find, for instance, that the phalanges of the digits arise from a continuous strand of procartilage; while more to the point are the conditions in the elasmobranchs. Here both upper and lower jaws (pterygoquadrate and Meckelian) form a continuum in the stage before the appearance of cartilage, and it is only with chondrification that differentiation occurs (*cf.* Sewertzoff, '97, fig. 1).

The point has also been made (Peters, '68,) that if the quadrate is such a large element in the sauropsida, we should hardly expect it to be such an inconspicuous element as it is in the closely related monotremes. The weak feature here is that it relates solely to adult structures, and exactly this same argument of relative size of parts has been advanced to prove exactly opposite conclusions. Thus Gegenbaur ('78, p. 467,) says: "The early differentiation and the, at first, relatively large size of the auditory ossicles, shows that they must be regarded as skeletal parts, which in a lower stage were much mere developed in size."

Those who deny the incudo-quadrate homology, have to face the question as to what has become of the quadrate—so promi-

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nent in all other vertebrates—in the mammals. To this two answers have been suggested. According to the one it is to be sought in the tympanic annulus (Gadow); according to the other (Albrecht, Cope, etc.,) it has disappeared in the region of the glenoid fossa.

In favor of the first of these views are several facts. In the first place the quadrate in the reptilia acts not only as the suspensor of the lower jaw, but it also forms the support of the anterior wall of the tympanic cavity, and, at least in living forms, the lining of the cavity is inserted upon it. In the anura Villy ('90) has described the annulus tympanicus as arising independently near the palatopterygoid, but Gaupp ('93 and '96), who has more recently gone over this matter in the frog, states that it is derived from the quadrate.

In my studies I have found but little bearing on the origin of the tympanic. At no time do I find any cartilaginous anlage, but the bone developes directly from membrane (fig. 4). Parker states ('85) that in Tatusia it is formed from cartilage with a scale of membrane bone in its outer side, and Flower ('85), possibly basing his statement on Parker's work, recognizes two elements in this bone. On the other hand, aside from my own observations, it would appear probable that in the higher mammals the cartilage has disappeared and the tympanic is purely a membrane bone (Hertwig, '88, p. 481). Gadow ('88, p. 477) recognizes this fact that the tympanic is not exactly equivalent throughout the whole of the mammalia, and yet a few lines below he says: "The os tympanicum of the mammals is equal to the quadrate + annulus tympanicus of the anura = quadrate proper + its metapterygoid region, or that the metapterygoid process of the anura = greater part of annulus tympanicus of mammalia; the quadrate proper of anura = that part of the annulus tympanicus which, in the young of Orycteropus, monotremata and marsupials, lies between the squamosal and the inner angle of the mandible."

Certainly homologies of such a character should have more detailed explanation. To be sure of these identifications one

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should follow the tympanic through its development from what was clearly a quadrate or derived from the quadrate, but I know of no such evidence. It may be that the cartilaginous tympanic of the lower mammals is the homologue of the element bearing the same name in the anura, in which case the membranous tympanic might possibly be the paraquadrate, but this is merely suggestion, and not by any means proved.

The evidence in favor of the other alternative—that the quadrate has been lost in the squamosal region—is even less satisfactory, although at the first glance the view seems plausible. This interpretation was first prominently brought forward by Albrecht ('83 and '84), but, as Baur has pointed out, the same idea was advanced in the writings of several of the older anatomists. Albrecht maintains that it is absurd to suppose that the articulation of the lower jaw in mammals is different from that in the sauropsida and ichthyopsida. In the non-mammalian group this articulation is by means of the quadrate, hence it follows that in the mammals the quadrate must be sought in the region of the glenoid fossa, where the lower jaw articulates with the skull. In support of this view he figures (83b) the malformed skull of an idiot, on one side of which a distinct bone extends down in front, from above the bony external auditory meatus to the articulation with the lower jaw. This bone he homologises with the quadrate of the lower forms, although he has not the slightest evidence to show that it is a cartilage bone rather than a membrane bone. Arguments from teratological conditions are sometimes of value, sometimes very misleading. One would like to know more about the history of the individual of which this skull was a part. Imbecility and a cranium malformed in this way on only one side are certainly suggestive of an artificial origin of conditions, and it is possible that the same injury which may have caused the loss of intelligence occasioned an irregularity of development of the squamosal.

Other evidence in this same direction is afforded by the monimostylic reptiles, where the quadrate loses its mobility and be-

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comes firmly fixed by the development of a membrane bone on its outer surface, this same membrane bone, to a greater or less extent, entering into the formation of the articular surface by means of which the lower jaw is fastened to the skull. Hence we have in these reptiles the first stages of a process to become completed in the mammals by the fusion of the membrane bone with the quadrate, when the latter would be lost in the squamosal.

Several objections suggest themselves to the acceptance of such a view. In the first place confusion has been introduced into these homologies by the term squamosal. Gaupp ('94a) has shown that the so-called squamosal of the sauropsida is not the homologue of the squamosal of the mammals, but that it is in reality a distinct bone, to which he has given the name of paraquadrate. Hence fusion of quadrate and paraquadrate would not result in the squamosal of the mammals, for the squamosal of this latter group has its perfect homologue in the non-mammalian groups. Again, no one has brought forth any embryological evidence to show that the quadrate has been lost in the squamosal region. The quadrate is a cartilage bone. If it has disappeared in this region we should expect to find cartilage here in embryonic stages, but no one has as yet found a trace of cartilage anywhere near the glenoid fossa. Another objection, though of less weight, lies in the character of the articulation already referred to. In amphibia and sauropsida the face of the quadrate for articulation with the lower jaw is convex, while the corresponding face of the articulare is concave. In the mammals the conditions are exactly reversed ; the condyle of the lower jaw is convex, while the glenoid cavity is concave.

These objections, which have just been stated, are by no means to be ignored, but there remains one far more important. In every non-mammalian group the articulation of the lower jaw takes place by means of the proximal end of Meckel's cartilage, or by means of a distinct bone (articulare) derived from it. In the mammals, on the other hand, the Meckelian does not come anywhere near the glenoid fossa, but its proximal end extends

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far behind this point, to its articulation with the incus, and this articulation, as was pointed out above (p. 224), corresponds exactly in its character to the quadrate-articulare joint of the non-mammalian forms.

I think that there is no escape from the conclusion that the articulation of the lower jaw in mammals is not homologous with that in lower forms. We cannot recognize in the mammalian lower jaw any bones to be regarded as either articulare or angulare. The relations of Meckel's cartilage, which lies far below the point of articulation, forbids us to regard the condyle as the articulare or to think that the quadrate can be hidden in the squamosal region. The accounts given by the older writers of the centres of ossification, as well as the more recent papers by Masquelin ('78) and Brock ('76), of the development of the lower jaw, are very unsatisfactory. Parker ('85, '85a) has given more definite evidence; and in some points of fact I can confirm him. Thus I find at least two distinct bones in each half of the lower jaw, while Parker recognizes a third. I agree with him in regarding two of these as the dentary and splenial; he calls the third the coronoid. Besides these bones which enter into the lower jaw a fourth membrane bone is formed on the lower side of the Meckelian, behind the jaw proper (p. 226), which gives rise to at least a part of the processus folianus of the mandible. I agree with Parker in calling this the angulare. In the marsupials Parker finds also a supra-angulare. Aside from Parker I find no one who has paid any attention to the possible morphological bearings of the cartilages which give rise to the ascending ramus and condyles of the lower jaw. These are large hyaline cartilage plates, which pass outside the Meckelian and do not in any way connect with it. It may be that Parker's suggestion that these represent the labial cartilages of the elasmobranchs may prove correct, in which case we would have the skeletal foundation for a new articulation of the lower jaw. Against this view, however, may be urged their late appearance in ontogeny, and, so far as my knowledge extends, their absence from other vertebrates higher than the elasmobranchs.

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MALLEUS.

The body of the malleus is developed from the proximal end of Meckel's cartilage. At first it is scarcely larger than the rest of the tract, but with increase in age it becomes considerably enlarged, while the more distal portions scarcely gain in size. At first, as has been said above, it is widely remote from, and has no connection with that part which I have called the manubrium, but soon procartilage, and later, cartilage, is developed connecting the two. I think there is no escape from the conclusion that the malleus is a compound structure, and that, as I have already stated, the probability is that it represents two gill arches. I have not followed the development through to the time when the malleus loses its connection with the rest of the Meckelian, but in pigs 80 mm. in length, when ossification is well advanced and the lower jaw has its definitive form, the malleus is still continuous with the rest of the arch,

This fact, however, does not in the least interfere with the view that the body of the malleus is to be regarded as homologous with the articulare in the non-mammalian groups. Gadow ('88, p. 479,) has advanced the argument that "the malleus cannot be the articulare, because the articulare is an ectochondral bone, like the other bony parts of the mandible, while the malleus is a cartilage bone." In this I think that Dr. Gadow has made a mistake, for all the other authorities at my command regard the articulare as cartilage bone, and thus place it in strong contrast with all the other bones of the lower jaw of the non-mammalian forms. It is possible that the peculiar method of ossification of cartilage which occurs in the amphibia has led him to this view, for there ossification of the visceral arches starts first as ectochondral bone, and only later invades the cartilage. It is difficult to imagine any way in which a membrane (dermal) bone could be intercalaled between the cartilaginous articular surfaces of the lower and upper jaws.

Again, Gadow says, "provided that the malleus is the modified upper part of Meckel's cartilage then the incus cannot be the homologue of the quadrate because of the impossibility of

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intercalating the quadrate as an incus into the ossicular chain as a link between the stapes (hyomandibula) and lenticulare (sympletic) and the malleus (articulare)." But, as has been pointed out before, almost exactly this impossibility does occur, as comparative anatomy would teach us to expect, in many urodeles, where the quadrate is intercalated (though not as a functional incus), between stapes (hyomandibula) and the articulare.

Now since the quadrate of the non-mammalian groups acts as a suspensor of the lower jaw, and this latter articulates with it by means of a cartilage or cartilage bone—the articulare—every known fact goes to the support of the view that the body of the malleus (*i.e.*, the caput of human anatomy, is the articulare, and this homology receives additional confirmation in the shapes of the articular surfaces already referred to (pp. 224 and 243).

The articulare, however, is not exactly equivalent to the malleus, for in the latter the manubrium is distinct in origin, and these two parts are only secondarily united by the formation of a cartilaginous connection in the region of the collum of human anatomy. Again I am strongly inclined to regard the bone described (p. 226), as forming part of the processus gracilis of the malleus, as the angulare of the non-mammalian forms.

THE PHYLOGENY OF THE OSSICULA AUDITUS.

We may now review in outline the various phases by which it seems possible that the ear bones have been evolved. The primitive condition of the parts involved were more simple than is known to occur in any existing elasmobranch, not excepting the notidanidæ. In the primitive condition there were two gill clefts and a skeletal arch between the hyoid and the mandibular arch, and corresponding to this a cranial nerve between the trigeminal and facialis, while in earlier stages head cavities and neuromeres were in full accord. Of all these features, except of gill cleft, we still have evidence, either in ontogeny or in the adult, and there are some things which may be interpreted as remnants of the visceral cleft.

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The next stage is characterized by a union of the intermediate nerve with the facial (*cf.* Beard), a fusion of the internal end of the intermediate gill slits, while the outer end of the anterior one becomes closed, leaving the posterior opening to form the spiracle, the intermediate cartilage forming the spiraculare. In the hyoid arch hyomandibulare and hyoid proper are still in connection and there is no suspensor of the jaws. This stage is realized in the notidanidæ.

Next in order is the condition in the higher elasmobranchs where the conditions are the same as before, except that the upper part of the hyoid arch has separated from the rest and has intercalated itself as hyomandibula between the posterior angle of the mandibular arch (*sens. lat.*), and the wall of the cranium, thus giving rise to the suspensor of the jaws.

From this condition two lines of development may be pointed out, the one leading to the anura, reptiles and birds, the other to the urodeles and mammals. In both lines there is a differentiation of the quadrate from the posterior part of the upper half of the mandibular arch and with this the attachment of the suspensor is transferred to the dorsal surface of the quadrate which as yet is free from any fusion with the cranium.

In following out the sauropsidan line we notice the development of a tympanum from the outer part of the spiracular cleft which becomes closed at its distal end. The hyomandibula enters into connection with the inner ear by disappearance of a part of the outer wall of the otic capsule. More distally it extends outwards behind the tympanum and unites with the intermediate cartilage (extracolumella), to form the columella. With this extension it loses its articulation with the quadrate, traces of which persist in many lizards in the ligament connecting the processus internus of the columella with the quadrate.

In the line leading to the mammals the quadrate has retained its freedom and its articulation with the hyomandibula (stapes). The Meckelian cartilage becomes connected with the intermediate cartilage (manubrium), but membrane bones fail to develop around the proximal part, unless possibly, as has been de-

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scribed, a separate bone (possibly angulare), takes a part in the formation of the processus longus. With the formation of the new articulation of the lower jaw—possibly by means of the labial cartilages—the proximal part of the arch loses all its function as a part of the mandibular apparatus and is devoted solely to auditory purposes. In the urodeles the connection between hyomandibula and quadrate may persist, but, since the tympanum fails to develop, stapes and quadrate can have but slight functions as sound conducting apparatus, while I have found no evidence of the development of an intermediate cartilage in this group. The urodeles, farther, are peculiar in that the quadrate, before the appearance of bone, becomes anchylosed to the cranium by several cartilage bars which have been described by all students who have treated of the chondrocranium.

THE ANCESTRY OF THE MAMMALIA.

No single bone occupies a more important position in the discussion of the origin of the mammals than does the quadrate. Upon the answer given as to its fate in this group depends, in large measure, the broader problem of the phylogeny of the mammalia. It is not yet time finally to settle this problem, nor am I in position to discuss in a proper manner the various arguments that have been advanced for the different opinions which have been expressed. Since the evidence of paleontology must have great weight in the matter, the discussions have largely been upon an osteological basis, but it is to be noted that most of those who have participated have utterly ignored the differences between cartilage and membrane bones.

Soon after the acceptance of the theory of evolution and the introduction of genealogical trees, Huxley, arguing chiefly from cranial characters, came to the conclusion that the mammals had had an amphibian and probably a stegocephalan ancestry. This view obtained general acceptance until 1884. It must be remembered that, previous to this date, Owen ('76), basing his reasoning largely on the structure of the long bones, suggested that the mammals had come from the theromorphous reptiles;

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and that Cope ('78), had adopted the same view, advancing additional arguments in its favor.

This view of a reptilian ancestry gained greatly when Caldwell and Haacke (in 1884), rediscovered the fact that the monotremes were oviparous and ascertained that their eggs had a meroblastic segmentation. Now neither of these features are amphibian in character, but both are found in the reptilia, and they appealed far more strongly to embryologists than does the presence or absence of an entepicondylar foramen in the humerus. From that time to the present this view that the mammals have sprung from the reptiles has prevailed, and the list of features which have been interpreted as pointing in this direction—almost entirely osteological in character, have been greatly increased by the researches of Cope, Seeley, Osborn, Baur, etc.

I have not the familiarity with the fossil theromorphs to enable me adequately to discuss these points, some of which would apply equally well to the amphibia. It would seem, however, that in many of these speculations there was a chance for error in the confusion of membrane bones with cartilage bones, and again in the assumption that bones having the same name in different groups must be homologous without regard to their actual relationships.

In the first place the theromorpha are—although very old—much too specialized a group to serve as ancestors for the existing amniote fauna.* Among the earliest forms (Permian) there is a range of structure which can only be explained on the assumption that a large number of forms, truly reptilian in character, had preceded them. It is true that some show primitive characters in the stegocrotophic (Gaupp) skulls, and the notochordal vertebral column. On the other hand extensive specialization is shown in the teeth, the absence, or small development of an obturator foramen (which Wiedersheim has shown must have occurred with the formation of the pelvis), the presence of an os transversum in the skull, and especially in the relations of

*I may say that I arrived at this conclusion before reading the papers of Baur ('86 and '87).

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the quadrate. This last point involves the question which type of skull, monimostylic or streptostylic may be regarded as the more primitive.

Cope ('84), apparently regards the immovable quadrate as the more primitive condition in the ichtheopsida, for he places the holocephali at the bottom (the least specialized), and from these he traces out two lines, one leading through the elasmobranchs and ganoids to the teleosts, the other running through the dipnoi to the batrachia. In regard to this he says (p. 585), "In this phylogeny, the holocephali, which have not differentiated a suspensorium, are regarded as the primitive fishes although the living representatives display some specialized characters. . . The line to the right [in his diagram] continues the monimostylic character and passes into the reptiles whose primitive forms are also monimostylic. . . . In the later forms or streptostylicate reptiles of Müller the quadrate becomes freely articulated."

In this there are several important errors. In the first place the assumption that the monimostylic condition is the more primitive is at variance with every known fact relating to the comparative anatomy and embryology of the visceral arches. The streptostylic condition is surely primitive, and the monimostylic secondary. Again, according to the unpublished researches of Dr. Dean (Kingsley '99, p. 242), the monimostylic condition is only secondarily developed in Chimæra, the young being streptostylic. In amphibia and alligators in which the adult is monimostylic the young are streptostylic, and the fixed condition of the quadrate is effected only secondarily by the development of the paraquadrate, while on the other hand in the squamata and birds, in which, if descended from monimostylic forms, we should expect to find a monimostylic condition in the young, nothing of the sort occurs in development. It should be pointed out, in this connection, that the monimostylic skulls present in reality two types. In the one, illustrated by the holocephali, dipnoi and amphibia, the quadrate becomes fixed to the cranial walls by cartilage; in the other, exemplified by turtles and crocodiles, the fixation is secondary and due to the development of membrane

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bones. It should be noted that later Cope ('92, '96), gave up the genealogical tree of the paper just mentioned, and following Pollard ('91), and Kingsley ('92), adopted a crossopterygian ancestry for the amphibia, in which he has been followed by Dollo ('95) and Baur ('96).

Again, it should be pointed out that the method of fixation of the quadrate is not the same throughout the reptilia. One has only to read the papers by Cope and Baur (American Naturalist, 1895 and 1896) and Gaupp ('94a) to see this. Farther, it has yet to be shown that the squamosal described by Cope, Seeley, Osborn and others, as uniting with the quadrate in the theromorphs is homologous with the squamosal in the mammalia.

But these are minor points, and the same may be said concerning the presence or absence of an entepicondylar foramen, for this last is a structure that might well arise twice within the vertebrate phylum. The method of articulation of the bicipital ribs in both theromorphs and mammals—one head articulating with a diapophysis and the other with the centrum—may have more weight, but this cannot be decided until we have more definite knowledge concerning the homologies of the different parts of the vertebrae than we now have, for our accurate knowledge on these parts is scanty and our ignorance immense. For instance, it has yet to be proved that the vertebrae of the mammals are derived from the centra, those of the amphibia from intercentra (Cope).

More important than all these features—than the presence of two or three occipital condyles, than the absence of a parasphenoid—are the relations of the quadrate. I have shown above, that in every respect the incus meets the requirement of the quadrate. Nerve relations and relations to the tympanic (spiracular) cleft, show that it cannot have any homologies with any part of the sauropsidan columella. Its development from the same stroma as the Meckelian; its articulation with the skull and with the stapes (hyomandibula); the character of its articulation with the head of Meckel's cartilage; its extremely

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large size in embryonic stages;—all go to support this homology. Now, if this be the case, it is impossible to regard the monimostylic theromorphs as ancestors of the mammals. This view is further negatived by the fact that—excepting the difficulty of explaining the formation of a new articulation—there is nothing to show that the articulation of the lower jaw in the theromorphs is homologous with that in the mammals, while the whole relations of Meckel's cartilage oppose such an interpretation. There is nothing to show that the mammalian lower jaw contains any element of the reptilian mandible back of the dentary. In short, I cannot, with present knowledge, regard the resemblances of theromorphs and mammals—further than they are shared also by the amphibia—other than the results of parallel development.

The ancestor of the mammals must have possessed the following features:

(1) Pentadactyle feet with five tarsales; (2) rhachitomous vertebræ; (3) two occipital condyles borne on the exoccipitals; (4) a freely moveable quadrate articulating with the hyomandibula (stapes) and otic capsule; (5) membrane bones roofing over the origin of masseter and temporalis muscles in such a way as to admit the development of the zygomatic arch; (6) structures which by modification could give rise to mammalian hair; (7) bicipital ribs; (8) structures which could give rise to the external ear; (9) an undifferentiated tarsus.

While certain of these characters (1, 2, 5, 7) fit the theromorphs, they are equally applicable to the amphibia, and so prove nothing. The third point is of more importance. We find two occipital condyles in the amphibia, but, and this point is often overlooked, they are not homologous throughout this group. Thus in urodeles and anura these condyles are borne by the exoccipitals just as in mammals, while in many stegocephali (labyrinthodonts) the paired condyles are basioccipital in origin and the exoccipitals do not participate in their formation. It is greatly to be regretted that our ignorance is so scanty regarding the lower stegocephali (those of undoubted amphibian affinities—

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the labyrinthodonts may not be amphibia, *cf.* Seeley, '92), but here the occipital region was usually not ossified. In all existing and most fossil reptiles there is a single condyle which may be formed by the basioccipital alone or by basi- and exoccipitals together. In certain theriodonts, however, conditions simulating those of amphibia and mammals have been described, the occipital condyle being spoken of now as 'distinctly bilobate,' now as having the double condylar condition produced by the recession of the basioccipital portion which is still quite prominent. In other words, the double condyles of these theromorphs are supposed to have arisen from a single condyle, in which all three bones participated, by the recession of the intermediate (basioccipital) portion. The mammals however, show no sign, in development, of passing through any such stage. The condyles are restricted to the exoccipitals from the first, and the basioccipital shows no sign of participation in their formation. We can readily see how the reptilian condyles can be derived from those of the labyrinthodonts, but neither theromorphs or labyrinthodonts could have furnished those of the mammals.

The freely moveable quadrate does not occur in any existing amphibian, while it is firmly fixed in all groups of reptiles which are thought of as ancestors of the mammals. In the urodeles the articulation between stapes and quadrate does occur, and in these forms the chain from stapes to articulare is complete, as it is in mammals. Yet it is impossible that the mammals have descended from any form distinctly urodelan, nor is there any known stegocephalan which will meet the requirements of the case. Farther, we know of no stegocephalan which could have served as ancestor of urodeles or cæcilians.

The sixth feature, the origin of the hair, is very important. Until recently it has been assumed that this distinctively mamalian structure was to be homologised, like the avian feather, with the reptilian scale. Maurer ('92, '93) has shown that hairs and scales are totally different in structure, and he has advanced no little evidence to show that the only structures in lower vertebrates which could have given rise to hairs are the epidermal

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sense organs of the ichthyopsida, and especially those of the amphibian type. Here he has been able to show not only a general resemblance, but a homology, part by part. Now these lateral-line organs are not known outside of the ichthyopsida, and the only place where I have found mention of features which could be interpreted as suggesting the existence of these sense organs in the theromorpha or in any reptilia is the expression by Case ('98), who states on the authority of Seeley that there are "mucous canals" between the orbits and nares of Parieasaurus. However, I fail to find any such statement in the paper of Seeley ('92), while his figures, although showing a sculptured skull, shows no such grooves as are well known in the labryrinthodonts and which are there regarded as connected with the lateral system. Against the supposition that these reptiles had these sense organs is one very important fact. We know only of these organs in aquatic animals, and in the existing amphibia they occur only in the aquatic stages and are lost, in urodeles, cæcilians and anura, upon the assumption of a terrestrial life. It would therefore appear that these structures can only function in an aquatic medium; hence on *a priori* grounds we would be led to assume that Parieasaurus and the other theromorphs could not have had these epidermal sense organs.

In all mammals, some aquatic types excepted, there are external ears, and everyone who has speculated upon these structures has sought to derive them from opercular structures like those of the teleostomes; and Ruge ('97) shows that the cartilages of the external ear and the meatus in the monotremes are derived from the hyoid arch, a view which fits in with the view that these are modified branchiostegals. Now it requires a considerable stretch of the imagination to suppose that opercular structures persisted in the theromorphs, while the absence, so far as is known, of corresponding cartilages in the region of the external meatus of existing reptiles and amphibia, renders it probable that these cartilages were lacking in the theromorphs. Existing mammalia and sauropsida are strongly marked off from

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each other by their tarsal structures. In the mammalia the tarsal joint is chiefly developed between the tibia and fibula on the one hand, and the proximal row of tarsal bones on the other. In the sauropsida the joint lies between the proximal and distal rows of tarsals; it is intratarsal. The amphibia clearly show a type of foot structure from which the mammalian conditions can be derived. It is greatly to be regretted that we do not know more about the foot of the theromorphs, but in Clepsydrops as figured by Cope ('89a), and Parieasaurus (Seeley '92), the appearances are strongly sauropsidan. It should be remarked, however, that in Parieasaurus the tarsal elements were dislocated when found.

There is another series of mammalian characters which are apparently opposed to a reptilian ancestry, since they occur in no existing reptiles, while they do occur in the amphibia. Still, since these are confined to the soft parts and cannot be preserved in the fossils, the evidence which they give is not absolute, like that of the quadrate, but is merely cumulative in character.

As embryology fifteen years ago gave strong support to the reptilian ancestry of the mammals, so today it offers even stronger evidence of an ancestry from the amphibians or forms allied to them. Hubrecht ('97), in his studies of the amnion and trophoblast, points out that these structures cannot be derived from any known type of reptilian egg, while the eggs of the amphibia possess structures which can be used to explain the way in which the peculiar fœtal envelopes of the mammals arose.

The thoracic duct affords another feature pointing towards amphibian rather than sauropsidan ancestry. In the mammals, as is well known, it is the left duct which persists, while in the sauropsida it is the right which is functional in the adult. These conditions point back to an ancestry in which paired ducts were present, but in the urodeles, according to the unpublished observations of Dr. F. D. Lambert, both right and left ducts are present in the larvae, but the right is much smaller than the other from the first, and it disappears at a very early stage.

Beddard notes ('84), the presence of an anterior abdominal vein in Echidna and says: "It is perhaps important to note that

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Echidna agrees with the amphibia and differs from the lacertilia [in] that the left of the primitively two allantoic vessels, instead of the right is persistent."

Klaatsch ('92) recognizes that the mesenterial structures and the peculiar arrangement of the superior mesenteric artery of the mammals, are unlike those of reptiles, and concludes "dass sie bezüglich der Mesenterialbildungen und der Anhangsorgane des Darmscanales an sehr primitive Formen angeschlossen werden mussen, an Formen welche sich bereits unterhalben der jetzt lebenden Amphibien von gemeinsamen Chordaten-Stamme abzweigten;" and farther: "Somit liefern auch die Mesenterialbildungen zur Frage nach der Phylogenese der Säugethiere ein Beitrag in dem Sinne, dass die Wurzel derselben viel tiefer gesucht werden muss, als dies heut zu Tage noch vielfach üblich ist."

From all of the foregoing we may conclude that no reptile has yet been found which in any way will fit the requirements for the ancestor of the mammalia; but that all known facts point rather to a line of descent from forms allied to the amphibia. There is, however, no amphibian which will meet the necessities of the case, but that we must go back to the common stock from which the known stegocephali, the urodeles and the cæcilians have sprung. We have as yet knowledge of no such forms, but we must remember that when the first known stegocephali appear the group is already well differentiated, and we have no record of the stages which must have been passed through between the crossopterygian ganoids and the evolution of the pentadactyl limb. The recent announcement by Marsh of footprints in the Devonian show that there must have been a quadrupedal fauna earlier than any of which any skeletons are at present known.

In conclusion it may be said that the ear bones afford no support for the view advanced by Mivart ('88), and partly accepted by other writers, that the mammals are a polyphyletic group, the monotremes having had one ancestry, the other orders another. The often described 'columelliform stapes' of the monotremes has no value as an index of sauropsidan affini-

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ties, nor can the teeth and mammary glands which form the basis of Mivart's argument, decide the matter.

SUMMARY.

(1) In urodeles and cæcilians the stapes arises independently of the otic capsule, and shows no trace of connection with the hyoid. It may be connected with the quadrate by ligament (Caducibranchiata), or it may articulate directly with this element (Phanerobranchiata, Derotremata, Gymnophiona). No tympanum is developed, and there is no columella formed.

(2) In the anura tympanum and columella occur. The columella is formed of three elements—stapes, pseudoperculum and extracolumella. The stapes arises as a chondrification distinct from otic capsule and hyoid; the pseudoperculum in the posterior wall of the tympanic cavity, and the extracolumella in the tympanic membrane. A tympanic annulus, forming a support to the anterior wall of the tympanic cavity, arises as an outgrowth which soon separates from the quadrate.

(3) In the lizard tympanum and columella are developed. In the columella but two elements—stapes and extracolumella—are recognized. The stapes is developed from the same stroma which gives rise to the hyoid, and therefore these are to be regarded as parts of one continuum. The conditions in lizards alone does not settle the question as to whether the stapes is hyomandibular in character, but comparisons with other forms render this view probable. The extracolumella arises as a distinct element, which later fuses with stapes. This element apparently represents a rudimentary branchial arch, and is bounded before and behind by rudiments of gill clefts. Ligamental or cartilaginous connections may occur between extracolumella and lower jaw. The columella lies behind the tympanic cavity and between hyomandibular and chorda tympani nerves. Pterygoid, quadrate and Meckelian cartilages arise from a continuous stroma, and are only differentiated upon the formation of cartilage. The external auditory meatus arises from the rudiments of the second external gill cleft. Ligamentary connections may occur between the processus descendens and the quadrate.

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(4) In the alligator as in the lizards, the quadrate is free until after the appearance of bone; it is united to the cranium later by the development of the paraquadrate. There is a cartilage band between the extracolumella and the proximal end of Meckel's cartilage. This is not a backward extension of the Meckelian, but is to be compared with the strip of cartilage which in the mammals unites the manubrium to the body (caput) of the malleus. In other respects the alligator closely resembles the lizard.

(5.) The stapes in the pig developes in continuity with the hyoid arch, but loses its connection upon the formation of cartilage. I have seen no evidence of the formation of a distinct basilar plate.

(6.) The incus arises from the stroma of the mandibular arch. It becomes distinct in the cartilage stage and develops an ascending process for articulation with the otic capsule, a stapedial process for articulation with the stapes, while its lower surface for articulation with the malleus is a rounded ridge. The whole structure is pre-tympanic, and in front of the chorda tympani nerve, and cannot be compared with any part of the sauropsidan columella. It every respect it fulfils the conditions demanded of the quadrate.

(7.) The malleus is composed of three parts, a body (caput) derived from the proximal end of Meckel's cartilage, and corresponding topographically with the articulare of non-mammalian vertebrates; a manubrium derived from a cartilage intermediate between hyoid aud mandibular arches, and only secondarily united to the caput by cartilage; and a membrane bone developing into at least a part of the processus gracilis (pr. Folianus).

(8.) The auditory chains of reptiles and mammals are homologous in their proximal and distal elements; stapes with stapes; extracolumella with manubrium. The connection between these is accomplished behind the tympanum in the sauropsida by a union of stapes and extracolumella. In the mammals the connection is made in front of the tympanum by means of the quadrate (incus).

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(9.) The tympanic annulus in the pig is purely of membrane bone.

(10.) There is not the slightest evidence of the loss of the quadrate in the mammals in the region of the glenoid fossa. On the other hand, the quadrate is fully accounted for in the incus. The articulation of the lower jaw of the mammals is a new formation, without any homology with the articulation of the lower jaw in the non-mammalian vertebrates; and both articulare and angulare are to be recognized behind this articulation.

(11.) The mammals have not descended from theromorphous reptiles, but their ancestors must be sought in forms with amphibian affinities, but more primitive in structure than any known stegocephalan.

POSTSCRIPT.

Since this paper was in type two important articles bearing on the ear bones have appeared. One of these by Bernard Weil.* I know only from a brief abstract by H. F. O[sborn] in Science for Jan. 19, 1900. According to this abstract Weil maintains that the quadrate is not represented in the chain of bones of the mammalian ear "for according to his observations the quadrate belongs not to the mandibular arch from which the mammals derive their ear bones, but to the palatoquadrate bar." I cannot but think that Weil has been misled by an erroneous conception of the visceral arches, as well as by the hypothesis that the mammals have had a reptilian ancestry. Palatoquadrate and Meckelian both belong to the first or mandibular arch, the palato-pterygoid portion being but slightly developed in the mammalian chondrocranium. A study of the development of the mandibular arch in elasmobranchs, urodeles and reptiles would have shown him that his position was untenable, and that primitive connection of incus with Meckelian was not in the least incompatable with quadrate homologies.

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*Development of the ossicula auditus in the opossum. Annals N. Y. Acad. Sci., xii, no. 5, pp. 103-118. This paper has not been received in any of the libraries in Boston.

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The second paper, by Gaupp,* is a detailed analysis and summary of our knowledge of the ear bones. In its general features it is in close accord with the views of structure and homology adopted in the present article, although, as might be expected, there is variance upon minor points. Gaupp, like myself, has paid no little attention to the chorda tympani as indicative of the presence or absence of homology and he concludes that "die von Reichert begründete Lehre, dass der Hammer als Articulare, der Amboss als quadratum der übrigen Vertebraten aufzufassen sei, erwies sich als unanfechtbar." He regards the tympanic membrane as not exactly homologous in mammals and sauropsida and thinks that the articulation of the lower jaw of the mammals is a new formation.

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*Ontogenese und Phylogenese des schallleitenden Apparates bei den Wirbeltieren. Merkel und Bonnet's Ergebnisse der Anat. u. Entwick. Bd. viii., pp. 990-1149, 1899.

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EXPLANATION OF FIGURES.

REFERENCE LETTERS.

a, angulare.
b[1], *b*[2], branchial arches.
bb, basibranchial.
bv, blood vessel.
ct, chorda tympani.
d, dentary.
em, external meatus,
eu, Eustachian tube.
ex, extracolumella.
f, facial nerve.
fo, fenestra ovalis.
g, Gasserian ganglion.
hm, hyomandibular nerve.
hy, hyoid.
i, incus.
il, ligament from columella to Meckelian.
j, jugular vein.
l, labyrinth.
m, Meckel's cartilage.
mt, temporalis muscle.
mu, manubrium.
mus dig., digastric muscle.
oc, otic capsule.
pi, processus internus.
po, pseudoperculum.
pt, pterygoid.
q, quadrate.
s, stapes.
sa, stapedial artery.
t, tympanic annulus.
tc, tympanic cavity.
v, fifth nerve.
x, Columellar-Meckelian ligament.

Figure 1. Reconstruction of ear bones and related parts of Pipa, after the metamorphosis.

Figure 2. Reconstruction of visceral arches of an early stage of the lizard.

Figure 3. Parasagittal section of lizard in the same stage as figure 2.

Figure 4. Transverse section of otic region of pig of 72mm., passing in front of the main chain of ear bones, and showing the angulare, tympanic annulus, and the squamosal behind the glenoid fossa.

Figure 5. Reconstruction of ear bones and related parts in pig of 72mm. Notice the pit in the wall of the otic capsule for articulation with the posterior process of the incus.

Figure 6, 6a. Reconstruction of visceral arches of pig of 15.5 mm.

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Figure 7. Parasagittal section of pig of 18mm.

Figure 8. Transverse section of pig of 72mm. passing through the stapes; *i. e.*, some distance behind fig. 4.

Figure 9. Reconstruction of ossicles in pig 20mm. long.

Fig. 10. Reconstruction of auditory region of a lizard, showing the relations of the columella to the branches of the facial nerve.

Figure 11. Parasagittal section of alligator.

Figure 12. Posterior view of model shown in fig. 10.

Figure 13. Relations of tympanic cavity to columella in lizard, forming the basis of fig. 10.

Fig. 14. Relations of ossicles and nerves in pig 20mm. long. Compare with fig. 10.

Figure 15. Parasagittal section of young lizard, showing the early relations of the extracolumella to the grooves (vestiges of gill clefts?) on the outside of the neck. By oversight the leaders were omitted from the drawing; the extracolumella lies between the two grooves on the lower margin; the external end of the tympanic cavity is indicated by the oval in the centre of the figure.

Figure 16. Reconstruction of the auditory region in the alligator.

Figure 17. Section through the tympanic region of a lizard, showing the invasion of the tympanic cavity by the columella (*c*) from behind.

Figure 18, Posterior view of ossicles of pig of 20mm., drawn from the same model as fig. 14.

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THE DEVELOPMENT OF THE EYE MUSCLES IN ACANTHIAS. ARTHUR B. LAMB.

THE CRANIAL NERVES OF AMPHIUMA. BY J. S. KINGSLEY.

THE SYSTEMATIC POSITION OF THE CÆCILIANS. BY J. S. KINGSLEY.

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TUFTS COLLEGE STUDIES, No. 7.

THE DEVELOPMENT OF THE EYE MUSCLES IN ACANTHIAS.[1]

BY

ARTHUR B. LAMB.

These studies were undertaken at the suggestion of Dr. J. S. Kingsley and were carried on during the year 1899-1900 under his direction, at the Biological Laboratory of Tufts College.

My specimens were killed either in aqueous corrosive sublimate or in Davidoff's corrosive-acetic mixture. Delafield's hæmatoxylin was principally used as a staining agent. Wax reconstructions were made according to the method of Born. My results are largely but confirmatory of those of Van Wijhe, Miss Julia Platt, Hoffmann and Neal. It is hoped, however, that a presentation of the subject freed from externals may, together with the series of reconstructions submitted, assist in the comprehension of the process of development.

The discovery that in selachii the eye muscles are developed from the epithelial walls of the 1st, 2nd and 3rd head somites was made by Marshall. His results have been repeatedly confirmed, and there can be no reasonable doubt of their validity. I use the term "somite" advisedly, being convinced that in Acanthias the head cavities are comparable with trunk somites. Neal, **98**, p. 187, presents an excellent summary of the evidence on this point. A history of the development of the eye muscles is therefore a history of the origin and differentiation of these head somites. At this point I wish to call attention to the very detailed account of the early history of these somites, presented by Hoffmann, **96**, in his "Embryology of the Selachii."

ANTERIOR SOMITE.—Before passing to a consideration of the eye muscle somites proper, I propose, for the sake of completeness, to consider the anterior somite. Van Wijhe saw (**82**, p. 13), in the single specimen of Galeus at his disposal, on either side of the head, anterior to the 1st or premandibular somite, a slender cavity with distinct and

[1] Reprinted from THE AMERICAN JOURNAL OF ANATOMY, Vol. I, No. 2, pp. 185-202.

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thickened walls. He homologised this with the anterior prolongation of the first somite observed by him in Pristiurus and Scyllium. He therefore considered it as merely a secondary subdivision of that cavity.

Miss Platt, 91, observed similar cavities in Acanthias, and to her is due the name of "anterior head cavities"; it seeming unwise to alter the numbering of the remaining head somites for the sake of a pair of somites which are only known to occur in two forms. It also de-

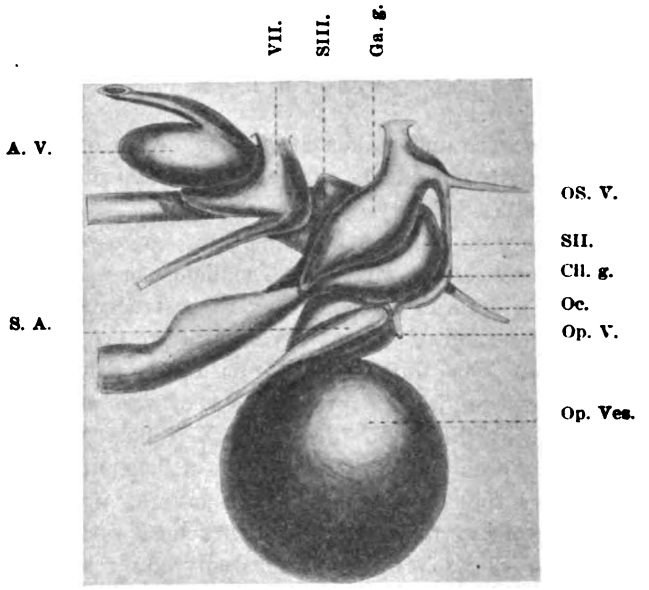

FIG. 1.—Reconstruction of auditory and optic vesicles, ganglia of fifth and seventh nerves and the anterior, first, second and third somites of the right side of an Acanthias embryo, 12½ mm. total length. Lateral view.

serves mention that Zimmermann, 91, p. 113, recognized, in the same year and quite independently of Miss Platt, the presence in Acanthias, of this somite. According to Miss Platt, the archenteron, which extended forward to the anterior neuropore as a solid mass of cells, was divided into an anterior and a posterior part by the down-growing infundibulum. Both parts grew laterally; the anterior forming the anterior head somite, the posterior the 1st or premandibular somite. Hoffmann was able to add to this the observation, that the down-growing *anlage* of the infundibulum not only divides this process of the archenteron into an anterior and a posterior part, but that it also sub-

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divides the anterior part into three smaller portions: one axial in position, two lateral and paired. From these lateral portions develops, on either side, the anterior head cavity of Miss Platt. Of the axial portion as much as lies beneath the infundibulum is aborted, while its anterior part persists and forms a connecting stalk by which the somite of one side is joined with that of the other. This connecting stalk is similar to that (*C. st.* in figures) which joins the first (premandibular) somite of one side with that of the other. The only difference is that there we have a canal, while here we have a loose and solid strand of

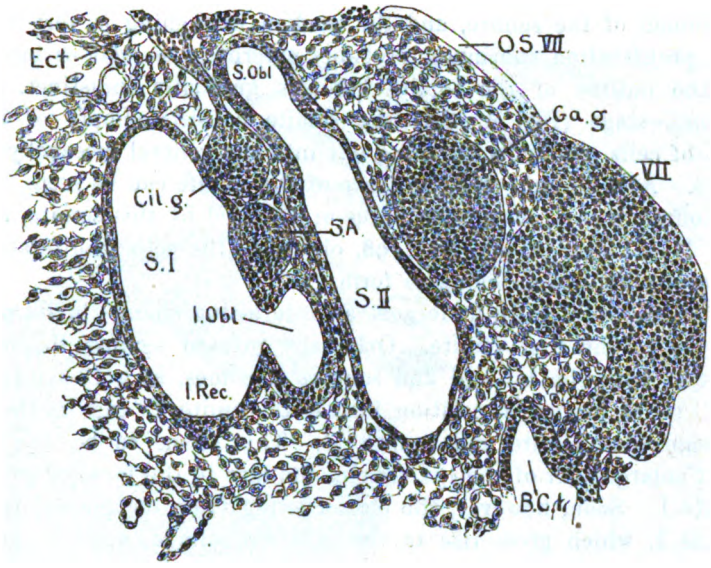

FIG. 2.—Parasagittal section of somites A, I and II of Acanthias embryo of 16 mm. total length showing the early differentiation of muscles inferior and superior obliquus and inferior rectus.

connective cells. It will be seen that Hoffmann differs from Miss Platt, simply in the recognition of an axial portion which later gives rise to a connecting strand. Stages in which 29-33 somites were differentiated showed very clearly the presence of this axial portion as described and figured by Hoffmann. See also Minot's figures (01, pp. 82, 83).

At a 32 segment stage the somite is elongate in form, its main axis extending obliquely downward beneath the eyeball. It is smaller at its dorsal end, where the cells have assumed a somewhat epithelial arrangement, and a slight lumen is present. Ventrally, the somite consists of a

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large mass of cells rather loosely packed, and occupying the space between eye-ball and epidermis. The somite is pressed closely against the anterior walls of both the 1st and the overlapping 2nd somite.

As the embryo grows older the somite assumes a much more elongate form (Fig. 1). The lumen increases in size and extends far into the ventral process, while the walls become considerably thinner and but one cell in thickness; still, they never become so thin as those of succeeding head somites. At a fourteen mm. stage the walls have again become thickened. This is especially true of the median and posterior walls. At a later stage (16 mm.) the cells are being freely proliferated into the lumen of the somite, and the median thickening is very marked. This proliferation continues, probably externally as well as internally, for the outline of the somite becomes gradually indistinct. At a 19 mm. stage (Fig. 4, *SA*) the somite consists simply of a solid mass of cells, gradually thinning out into the general mesenchymatous tissue. At a 26 mm. stage no trace of the somite can be seen. While, as Hoffmann says, no muscle fibres are formed by this somite, still, as both Miss Platt, 91, and Neal, 98, observed, the cells proliferated into the cavity assume an elongate form.

The anterior somite undergoes an interesting change in its position relative to the first somite. Originally pressed against the anterior walls of both the 1st and 2nd somites it comes, at a 12.5 mm. stage (Fig. 1), to occupy a position lateral to somite I, and in the angle between that somite and somite II. This seems to be due to the great enlargement of the eye vesicle, and also to the forward growth of somite I. Soon, however, the outpocketing from the posterior end of somite I, which gives rise to the inferior oblique, appears, and this ultimately grows nearly around the anterior somite, so that this later somite occupies a deep depression in its wall (Figs. 2 and 3).

Neal, 98, p. 227, found at a 65 segment stage processes apparently extending from the ciliary ganglion to this somite. I have not been able to find such processes of whose nervous character I was certain.

FIRST, OR PREMANDIBULAR SOMITE.—The epithelial walls of this somite give rise to four of the six muscles of the adult eye. It is therefore preeminently the eye-muscle somite of the head. Balfour stated that this cavity was cut off from the anterior end of the cœlom by the formation of the first gill cleft. Marshall also held that it was cut off from the anterior end of the cœlom, but that this took place independently of the formation of the gill cleft. In Scyllium and Pristiurus, Van Wijhe found that the cavity was never in other than potential connection with the primary cœlom, arising independently of it

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from the undifferentiated mass of cells in which the notochord anteriorly ends.

In Acanthias, as was shown above in the history of the anterior somite, the down-growing infundibulum divides the anterior prolongation of the archenteron into an anterior and posterior portion. From the anterior portion the anterior somite develops. The posterior por-

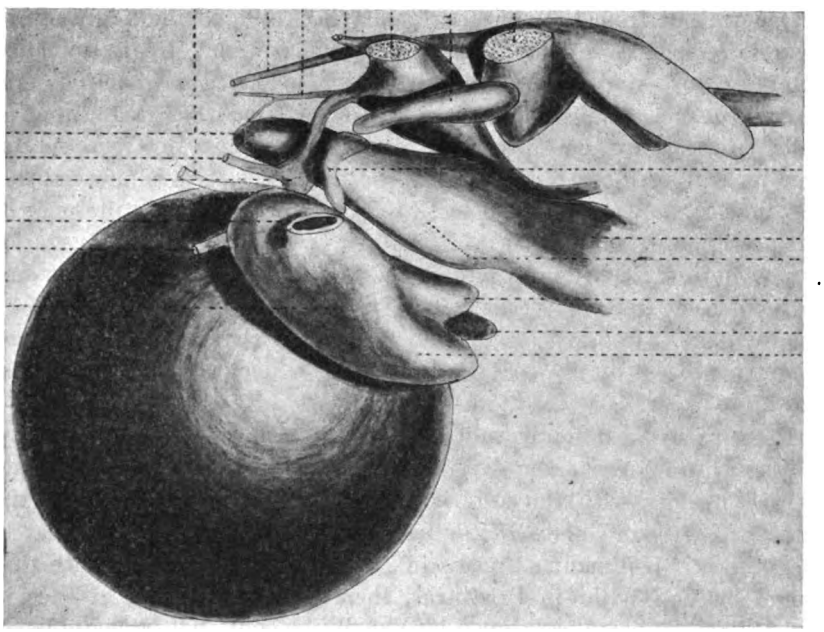

FIG. 3.—Reconstruction of optic vesicle, head somites and nerves of an Acanthias embryo, 16 mm. total length. Right side, medial view.

tion, growing laterally, gives rise to the first somite of either side, while axially it forms the connecting stalk or canal so characteristic of this somite (Fig. 3, *C. st.*). At a stage when 21-22 somites are differentiated, both the somite and the connecting strand are solid. This is still the case at a 29-30 mm. stage, except that in the connecting stalk a small cavity is visible. At a slightly later stage the number of these median cavities has increased. Miss Platt, **91**, homologised these with the median cavities described by Dohrn, **90**, in Torpedo.

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A considerable lumen can now be distinguished in the lateral somites. The median stalk is continuous at its middle with the notochord above and the alimentary canal behind. Hoffmann describes three processes arising at this stage (32 segments) from the 1st somite:

I. A process extending backwards and downwards, running close to, and parallel with, the visceral prolongation of the 2nd somite. He considered it probable that this process, although he had never seen a lumen in it, was comparable to the hollow process found by Zimmermann, 91, in Pristiurus, connecting the premandibular somite with the ventral cœlom. Neal, 98, p. 201 note, while confirming the presence of this "Zellstrang," was very certain that it was derived not from the mesoderm but from the neural crest, having followed the migration of neural crest cells ventrally into the mandibular arch. Neal also called attention to a similar strand of cells situated *posterior* to the visceral portion of the mandibular cavity. While I found that this strand of cells is apparently continuous with a slight outgrowth from the 1st somite, as figured by Hoffmann, this continuity seems to be more apparent than real. In the first place, I am able to confirm the presence of the posterior strand described by Neal. Further, I found this posterior strand not only continuous laterally with the anterior strand, but dorsally with neural crest cells. This is especially evident at a 32-33 somite stage. I therefore conclude with Neal that this "Zellstrang" is not a process of the somite, but is rather derived from the neural crest.

II. A process extending ventrally forward below the anterior cavity. A similar process was seen by Van Wijhe in Pristiurus and was homologised by him with the anterior head cavity of Galeus. Since the anterior cavity in Galeus is in all probability homologous with that in Acanthias, if Hoffmann's process in Acanthias is homologous with that found by Van Wijhe in Pristiurus, then, since both occur at once in Acanthias, the homology drawn by Van Wijhe could not be maintained. Hoffmann believed this to be the case.

I have been able to find but very slight evidences of this process. I am led therefore to doubt the homology drawn by Hoffmann between this process and the process described by Van Wijhe in Pristiurus. Consequently, I cannot on this ground take exception to the homology drawn by Van Wijhe between the process of the 1st somite in Pristiurus and the anterior somite in Galeus.

III. A process extending dorsally along the anterior surface of the 2nd somite. It is small in extent and transitory in appearance. I am inclined, here as before, to doubt the real continuity between this

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process and the somite, since it seems to me that it might equally well be derived from neural crest cells.

As the embryo develops, the median stalk is pushed away from the alimentary canal and around the end of the notochord by the intervening aorta. The notochord thus shifts its position from the dorsal wall of the median stalk to its posterior wall. Such is the compression

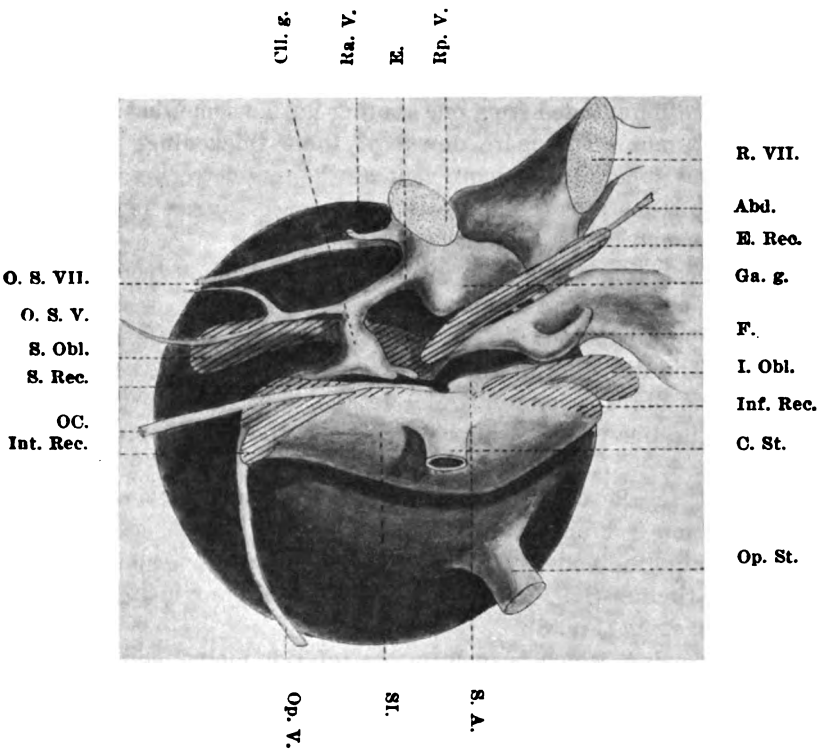

FIG. 4.—Reconstruction of optic vesicle, ganglia and somites of an Acanthias embryo, 19 mm. total length. Right side, medial view. The *Anlagen* of the muscles lined obliquely.

that exists in this region that the median stalk is nearly severed at the point of contact. The irregularly placed median cavities of the stalk now fuse together and finally assume connection with the lumen of the somite on either side. The lumen of the median stalk persists until a late stage, when the walls become mesenchymatous and the cavity is obliterated. The stalk persists, however, as connecting strand until nearly a 30 mm. stage (*C. st.* in Figs. 1-7).

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The thickenings of the epithelial walls which give rise to the four muscles, occur in general on the dorso-median walls. The first thickening appears on the more ventral end of the somite. This soon becomes a large outpocketing with thick walls (Fig. 3, *I. Obl.*). It is the anlage of the muscle obliquus inferior. This therefore is, as Hoffmann pointed out, the first of the oculomotor muscles to be differentiated.

The next thickening to appear is located very near the above-mentioned *anlage* of the inferior oblique. It gives rise to the muscle rectus inferior (Fig. 3, *Inf. Rec.*). At a later stage thickenings appear on the more dorsal end of the somite. These do not become well marked and differentiated from one another until a somewhat late stage, about 20-22 mm. The more dorsal of these thickenings forms the muscle rectus superior; the more ventral, the muscle rectus interior.

It will be seen from the above that the muscles arise in two pairs, one at either end of the somite.

The outpocketing which is to form the inferior oblique soon becomes constricted off from the somite. At a 19 mm. stage its lumen has nearly disappeared, and the muscle has assumed an elongate form (Fig. 3). The direction of the principal axis as well as the direction of its muscle fibres is longitudinal. In the adult the direction is also nearly longitudinal, but it will be seen from the series of reconstructions (Figs. 4, 6, 7, 8), that the originally anterior end has become posterior; i. e., the direction of the muscle is nearly reversed. This transformation is brought about by a revolution of the posterior end about the anterior end as a centre, combined with a general ventral shifting of the muscle. The adult condition is approximately reached at a 33 mm. stage (Fig. 8).

The thickening, which is to form the inferior rectus, and belonging to the same pair as the inferior oblique, at first extends parallel to that muscle and therefore in a longitudinal direction (Fig. 4, *Inf. Rec.*). At a 26 mm. stage it has turned through approximately a right angle, and runs in a general dorso-ventral direction (Figs. 6, 7, *Inf. Rec.*).

The thickenings which arise in the more anterior and dorsal end of the somite, and which give rise to the superior and internal recti, have only become clearly differentiated at a 25 mm. stage (Fig. 7). The internal rectus retains its nearly longitudinal direction; the superior rectus describes approximately a right angle about its posterior end. At a 33 mm. stage (Fig. 8) it has approximately reached its adult dorso-ventral direction. Except where the muscle thickenings have been formed, the walls of the somite retain their single layered epithelial character until about a 27-30 mm. stage, when they become converted into loose mesenchyme and the outline of the somite is lost.

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The musculature arising from this somite is innervated by the oculomotor. This nerve is differentiated at an 8 mm. stage. It arises, Neal, 98, from the ventral floor of the mid-brain, as processes from neuroblast cells in the ventral horn of this encephalomere. It extends backward to the ciliary ganglion and runs through it to the walls of the 1st somite. Neal, 98, p. 227, found, at a stage before the appearance of the oculomotor, processes extending from the ciliary ganglion to the somite, similar to those found in connection with the anterior

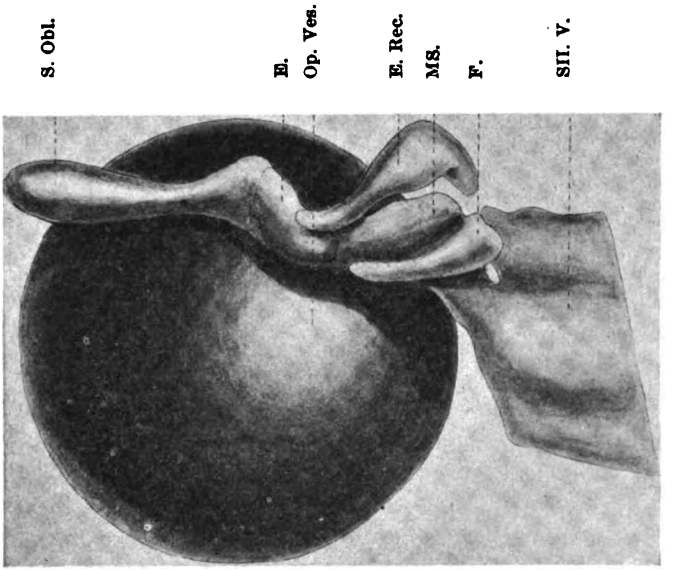

FIG. 5.—Reconstruction of optic vesicle and derivatives of the mandibular and hyoid somites of the right side of an Acanthias embryo, 22 mm. long, viewed from medial side.

somite. As in that case, I have been unable to convince myself that the fibres which seem to connect ganglion and somite are really nervous in character.

SECOND, OR MANDIBULAR SOMITE.—This somite is the largest in the head, and is characterized by the possession of a visceral portion connecting it with the ventral cœlom.

Hoffmann, 96, found this somite marked off by constrictions from the general body cavity at a 20 somite stage. A contracted lumen was present. At this stage the floor of the brain is pressed closely down upon the notochord and somite, but as growth takes place it draws

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away, and a considerable space is left beneath it. Into this space a proliferation of mesenchyme cells takes place from the anterior-median wall of the somite.

The walls of the somite at this stage are thin and single-layered, except in the median side, where the cells are higher and a tendency towards the formation of two layers is evident. Later, the median wall becomes thicker, and the area of mesenchyme proliferation more definite. The cells derived from this outgrowth are spreading out around the walls of the somite. This outgrowth seems to me to be

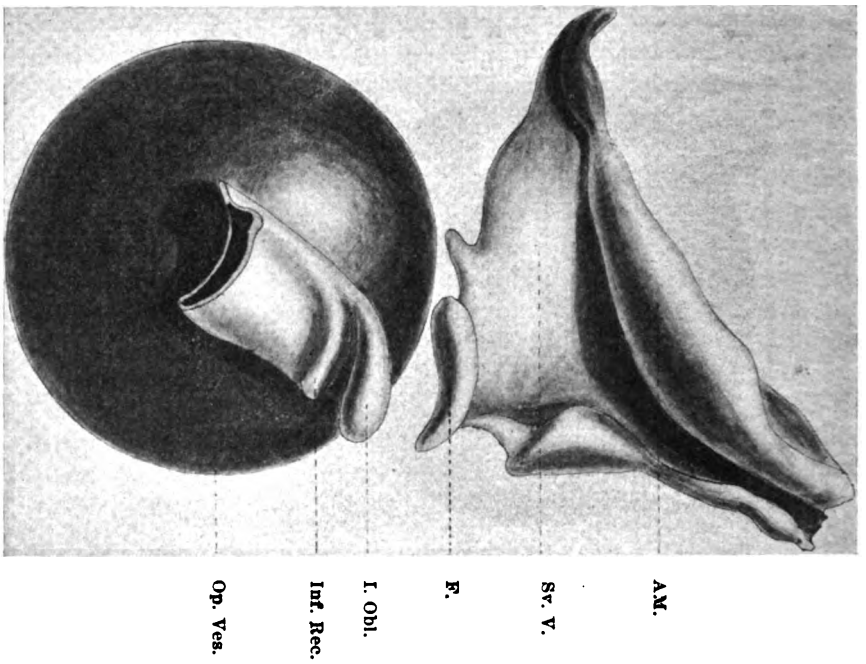

FIG. 6.—Reconstruction of optic vesicle and derivatives of the premandibular somite of an Acanthias embryo, 26 mm. total length. Right half, medial view.

comparable to a sclerotome of a trunk somite, both in position and in histological appearance.

At a 10 mm. stage the lateral, as well as the posterior median walls, have become very thin. This thinning out at posterior median wall continues, and soon the epithelial character of the bounding tissue is lost. This break, together with a constriction which gradually takes place, divides the somite at this point ultimately into a dorsal and a

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visceral part. At a 12 mm. stage the lumen of the one part is completely separated from that of the other. Until a late stage, however (24 mm.), the two parts are connected by strands of mesenchymatous tissue (Fig. 5, *MS.*).

For the sake of clearness I will treat the further development of dorsal and visceral parts separately.

Dorsal Part, or the Myotome Proper.—At a fourteen mm. stage a large outpocketing with slightly thickened walls is apparent at the anterior end of this part of the somite. This outpocketing is the anlage of the muscle obliquus superior. At the base of this outpocketing, on the median side of the somite, a thickening of the epithelium is evident. This is the anlage of a rudimentary muscle first mentioned by Miss Platt, and spoken of by her as "Muscle E." The walls of the remainder of the dorsal part are very thin.

Sixteen mm. stage (Fig. 3). The outpocketing giving rise to the superior oblique has become very thick-walled. "Muscle E" is well developed. The direction of its principal axis, as well as of its fibres, is longitudinal. It is not straight, however, but its anterior end is curved outwards.

From this stage on, those parts of the walls not forming muscles rapidly degenerate, and the lumen of the somite is usurped by mesenchymatous tissue. A contracted lumen, however, persists until a late stage in the anlage of the superior oblique muscle. The general direction of this muscle and of the fibres which are now present in it, is longitudinal. The whole muscle migrates forward, the posterior end becoming attached, while the anterior end moves ventrally. The muscle consequently comes to extend in a dorso-ventral direction (Figs. 4, 5, 8, *S. Obl.*). At a 19 mm. stage (Fig. 4) it is still longitudinal and still retains connection with "Muscle E" by a strand of connective tissue. This latter muscle has now reached its maximum development. The anterior end curves not only outward but upward as well, so that the direction of the muscle is approximately dorso-ventral. From now on this muscle undergoes degeneration. At a 26 mm. stage scarcely a trace of it remains.

Visceral Part.—At a 12 mm. stage the walls of this part, except where they are continuous dorsally with the somite proper, are closely compressed right and left. At the ventral end the walls are very thick, and constitute the *anlage* of the muscle adductor maxillæ.

At a 14 mm. stage an outpocketing appears at the dorsal end. This is the *anlage* of a rudimentary muscle which Miss Platt, 91, first recognized. Hoffmann, 96, considered this muscle identical with that de-

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scribed by Vetter, 74, and designated by him, muscle levator labii superioris. He does not, however, give any reasons for this view. Miss Platt was able to trace this muscle only until it came to occupy a position in close proximity to the inferior oblique eye muscle. She believed, however, that the muscle was permanent.

This outpocketing, as will be seen in the reconstructions, can readily be followed until a 26 mm. stage (Figs. 4, 5, 6, *F*). At a 22 mm. stage

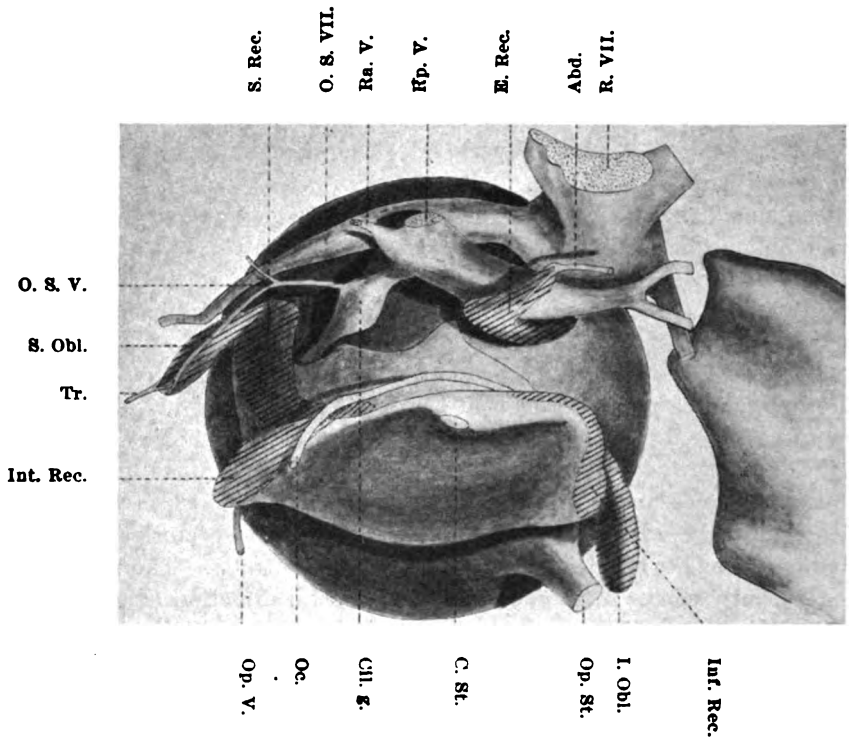

FIG. 7.—Optic vesicle, nerves and developing eye muscles of an Acanthias embryo, 27 mm. total length. Right side, medial view. The oblique lines indicate the parts of the somites which are being converted into muscles.

its walls are thin and enclose an extensive lumen. At a 26 mm. stage its lumen has disappeared and its constituent cells have become elongate and apparently muscular. The muscle is situated at this stage, as Miss Platt stated, close to the inferior oblique eye muscle. As will be seen in reconstructions, it is nearly continuous with the thickened ventral edge of the remainder of the visceral part. The cells of this

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thickened edge seem also muscular. At a 27 mm. stage I have been able to find only the very slightest remains of this muscle. Such a rapid degeneration seems, however, improbable, and requires, I feel, further investigation.

The superior oblique muscle derived from this somite is innervated in the adult by the trochlearis. This nerve, however, is the last cranial nerve to be differentiated, not appearing until a 21-22 mm. stage (Fig. 5). At a 16 mm. stage, as several investigators have shown, the small ramus ophthalmicus superficialis V. sends fibres to this somite. From this it might be inferred that motor impulses were originally transmitted to this somite by the 5th nerve. Neal considers this supposition untenable, since in embryos of but 19 mm. length, consequently before the appearance of the trochlearis, the ramus ophthalmicus superioris V. shows no connection with the muscle. While unwilling to contradict this latter statement and say that such a connection does exist, I should be even more unwilling, because of the *very* close proximity of muscle and nerve at 19-24 mm. stages, to say that such a connection does *not* exist.

THIRD, OR HYOID SOMITE.—This is the most posterior somite which contributes to the musculature of the eye, giving rise to the external rectus muscle. It is marked off from the rest of the body cavity merely by constrictions before and behind, at a time when the 7th somite of Van Wijhe is completely separated. This emphasizes the progressive development which takes place both forward and backward from a point in the neck region. At this stage its form and position is very similar to that of the four succeeding head somites. At a 22 segment stage a contracted lumen is generally visible. Neal points out that at this stage the somite is in every way comparable with a trunk myotome. It is plainly dorsal in its topographical relations to the notochord, dorsal aorta and dorsal wall of the alimentary canal. Mesenchymatous cells are plainly proliferated from a well marked area on its median wall, forming an outgrowth comparable to the sclerotome of trunk somites. The somatic wall is plainly epithelial and there is a well marked myocoel. Finally, the somite is, as will be seen later, innervated by a nerve which is generally recognized as comparable with the ventral root of a spinal nerve.

At a 28-30 segment stage this somite is completely separated from its neighbors. Its lumen has become well marked, while anteriorly the somite has assumed a bilobed appearance. At a 32 segment stage this lobation is especially evident. More marked growth now takes place in the middle and posterior part of the somite, and at the same time the walls there begin to lose their epithelial character.

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At a 10 mm. stage the lateral posterior end has become distinctly bilobed, and the more lateral of these lobes bears, in favorably orientated sections, a striking resemblance to the visceral portion of the 2nd somite. The disintegration of the epithelial walls of the main portion of the somite continues, while the more dorsal of the two anterior lobes has increased greatly in size. At a 13 mm. stage (Fig. 1) the main

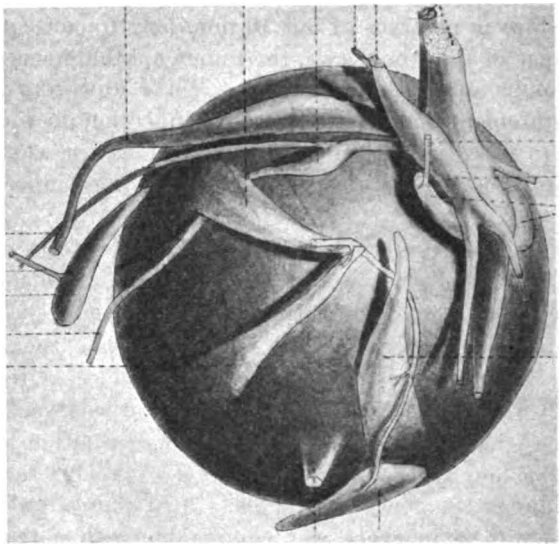

FIG. 8.—Optic vesicle, nerves and eye muscles of an Acanthias embryo, 33 mm. total length. Right side, medial view. The muscles have now nearly their definitive position.

portion of the somite, which is large and globular, is bounded merely by loose connective tissue which now rapidly fills up the lumen of this part of the somite. There is therefore remaining only the anterior prolongation or dorsal lobe, which consists mainly of elements derived from the median wall. This prolongation now grows rapidly and extends directly forward as an elongate pointed process. Its median dorsal wall is thickened, especially at the posterior end. There, as well

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as in the anterior portion, cells are assuming an elongate form and a longitudinal direction. The posterior end is indistinct in outline, and cells are evidently dropping off into the mesenchyme. By this degeneration at its posterior end, by growth of the muscle as a whole, and especially by the outpushing at its anterior end (Fig. 9, *E*), the whole somite moves forward, so that while originally located some distance away, it comes to lie in close proximity to the eyeball (Figs. 4, 5, 7, 8, *E. Rec.* Fig. 9, *a*).

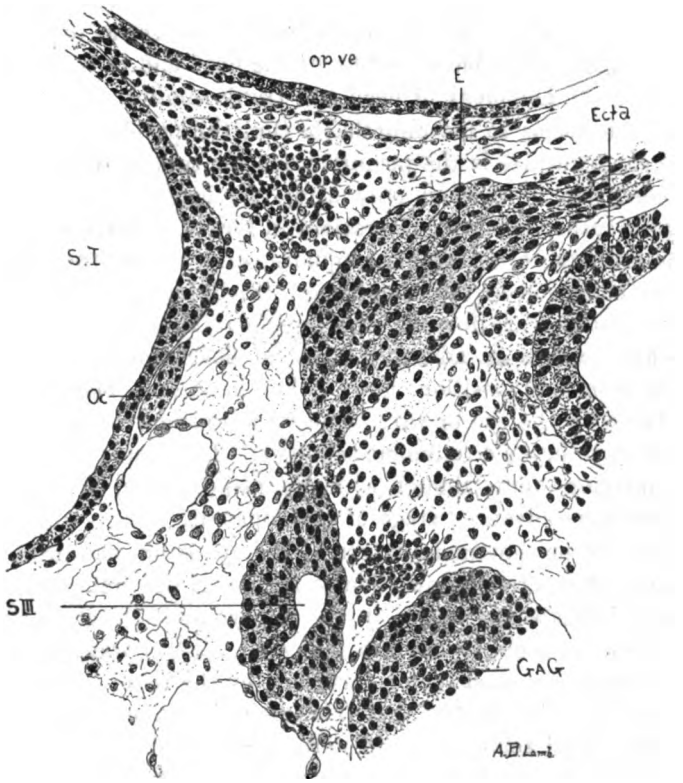

FIG. 9.—Part of transverse section of Acanthias embryo, 19-20 mm. total length, showing the proliferation of the external rectus muscle (E) from the hyoid (III) somite.

This somite is innervated by the abducens. This nerve is, as mentioned above, generally considered as homologous to the ventral motor root of spinal nerves. It arises (Neal, 98, p. 230) at a ten mm. stage from the floor of the hind brain at a point opposite the ear vesicle as an outgrowth from neuroblast cells in the ventral wall of encephalomere VII. The nerve gradually extends forward until it reaches its somite.

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CONCLUSIONS.

Broadly considered, it will be seen that the necessary mechanical relations between eyeball and muscle is secured: (1) by a forward growth of processes from the 2nd and 3rd somites, and the development of muscle fibres in them; (2) by a spreading out of the 1st somite around the eyeball and the development of muscles in its distal portions.

I wish to call attention to the fact, which so far as I know has not been noticed before, that the original direction of all the eye muscles together with "Muscle E" is longitudinal. This seems to me to represent an originally flexible condition of the head and to be an additional support for the homology of head and trunk somites.

Finally, it seems to me improbable that the present musculature of the eye in Acanthias is the primitive one for several reasons: (1) The adult condition is reached only after the constituent muscles have undergone rather extensive alterations in form and transfer of position. (2) The muscles do not all arise equally early, nor do they reach their definitive condition at the same time. (3) Before some of the permanent eye muscles are formed, one muscle ("Muscle E"), which later disappears, reaches an advanced stage of development. This muscle, from its form and position, must either have once been functionally connected with the eye or with some structure now lost, and of which not even an embryonic rudiment is known. The same reasoning applies to the anterior somite though with diminished force, since it does not reach the same advanced stage of development.

If then the present musculature of the eye is not the primitive one, it becomes an interesting question to inquire if the embryonic development will indicate any stages in the phylogenetic development. Two such stages, it seems to me, are indicated. 1st, a stage where if any eye musculature existed it was furnished by the anterior somite. This is indicated first by the fact that this somite is the only one which from its topographical relations could move the eye; and second, the longitudinal direction and serial arrangement of the remaining muscle *anlagen* indicate a jointed condition of the head and consequently a functional activity on the part of these muscles which would preclude any connection with the eye.

2nd, a stage at which four muscles moved the eye. These were the superior oblique, the external rectus, the inferior oblique and "Muscle E." These four muscles were arranged radially. "Muscle E" and the inferior oblique opposed one another, the former pulling the back of the eye dorsally, the latter, ventrally. The superior oblique and the

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external rectus opposed one another, the former pulling the back of the eye forward; the latter, backwards. This stage is reached in ontogeny at a length of 21-22 mm. (Figs. 4, 5, 6). The four muscles then have the rectangular radial arrangement described above. They have all reached approximately the same degree of differentiation, which is far in advance of the three remaining eye muscles.

These speculations, based solely on ontogenetic evidence, require confirmatory phylogenetic evidence derived from a study of forms lower than Acanthias.

REFERENCE LETTERS COMMON TO ALL FIGURES.

Abd., abducens nerve.
AM., *anlage* of muscle adductor mandibulæ.
A. V., auditory vesicle.
BC. I., first branchial cleft.
Cil. g., ciliary ganglion.
C. St., stalk connecting the premandibular somites of the two sides.
E., Temporary muscle derived from the mandibular somite; in Fig. 9, external rectus muscle.
Ect., ectoderm of dorsal surface of head.
E. Rec., externuis rectus muscle.
F., temporary muscle derived from the mandibular somite.
Ga. g., Gasserian ganglion.
I. Obl., inferior oblique muscle.
Inf. Rec., inferior rectus muscle.
Int. Rec., internal rectus muscle.
MS., mesenchyme connecting dorsal and visceral parts of somite II.
NC., notochord.
OC., oculomotor nerve.
Op. St., optic stalk.
Op. Ves., optic vesicle.
Op. V., ophthalmicus profundus branch of fifth nerve.
O. S. V., ophthalmicus superficialis branch of fifth nerve.
O. S. VII., ophthalmicus superficialis branch of seventh nerve.
Ra. V., anterior root of fifth nerve.
Rp. V., posterior root of fifth nerve.
R. VII., root of seventh nerve.
S. A., anterior head somite.
SI., *SII.*, *SIII.*, first (premandibular), second (mandibular), and third (hyoid) somites.
S. Obl., superior oblique muscle.
S. Rec., superior rectus muscle.
SII. D. & V., dorsal and ventral portions of somite II.
Tr., trochlearis nerve.
VII., seventh nerve.

All of the figures except 2 and 9 are drawn from wax reconstructions. The regions ruled on figures 4 and 7 are those portions of the somites which are being transformed into muscles.

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TUFTS COLLEGE STUDIES, No. 7.

[SCIENTIFIC SERIES.]

THE CRANIAL NERVES OF AMPHIUMA.*

By J. S. Kingsley.

The studies described below were begun ten years ago and were put approximately in their present shape two or three years later, but were then laid aside with the idea of including them as part of an article dealing with all systems in the head of Amphiuma. Various other matters have interfered with this project so that it has been thought best to present the account of the cranial nerves alone, since it is believed that they contain some features worthy of notice.

The work has been prosecuted in the usual manner by plotting the sections on cross-section paper, supplemented by wax reconstructions in the more complex regions. The following description is concerned only with topographical relations, the condition of the material preventing any detailed investigation of nerve origins or components.

For my material of Amphiuma I am indebted first to Dr. O. P. Hay, who gave me some specimens from the lot which formed the basis of his paper; second to the late Professor John A. Ryder, who turned over to me the material collected for him by Dr. Souchon of New Orleans. I have also young purchased from the Brimley brothers of Raleigh, N. C. I must also make acknowledgment here to Professor Robert Wiedersheim, since much of the investigation was carried on in his laboratory. Only one who has worked with him can have any adequate idea of his helpfulness, his kindness and his generosity of ideas and material.

* Papers from the Biological Laboratories of Tufts College, No. XXVIII.

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With the exception of the classical paper by Fischer ('64), the study of the nasal region by H. H. Wilder ('92) and a few almost incidental remarks by Osborn ('83), Hay ('90), and Davison ('95), and my preliminary paper ('92), nothing has been published upon the cranial nerves of Amphiuma.

THE OLFACTORY NERVE.

Lee ('93) has discussed the relations of the olfactory nerve in the lower vertebrates. In its extreme development he recognizes the following components: (1) A more or less sharply differentiated region of the cerebrum, the tuberculum olfactorium; (2) a long and slender tractus olfactorius uniting the more distal portions with the tuberculum; (3) the bulbus olfactorius in which are the glomeruli olfactorii and from which arise the fila olfactoria or olfactory fibres proper. Tuberculum, tractus and bulbus constitute the lobus olfactorius. In the Amphibia the lobus is not differentiated but is united with the cerebrum and the fila pass out from this region.

In Amphiuma the glomeruli are easily recognized in a long narrow region, extending along the lateral sides of the cerebral hemispheres as far back as the level of the eye. The ganglion of the olfactorius can be traced from this point back to the level of the posterior margin of the middle of the eye. This ganglion is a double structure, consisting of dorsal and ventral portions, the dorsal extending the farther backward. In front the glomeruli extend some distance beyond the point of emergence of the olfactory nerve; in fact, almost to the extreme tip of the brain. From the posterior part of the glomerular region a nerve arises which passes forward, closely appressed to the side of the brain, until it reaches and unites with a root more anterior in origin, when the two unite into a single trunk. I have not been able to follow the fate of the fibres derived from these two roots. The common trunk almost immediately separates into two portions (one upper and outer, the other medial and more ventral in position) before passing through the walls of the skull. On entering the nasal capsule the two rami pass between the ramus nasalis internus (*infra*) and the upper part of Jacobson's gland, and are soon broken up into fine branches which are

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distributed respectively to the dorsal and ventral portions of the olfactory epithelium, the medial portion of the epithelium being innervated by the ventral ramus.

The condition of the olfactorious of Amphiuma is much like that described by various authors for other urodeles (Diemyctylus, Gage, '93; Triton, Burckhardt, '91; Spelerpes and Salamandrina, Lee, '93) so far as double roots are concerned. Fish ('95) on the other hand describes only a single olfactory root in Desmognathus as I did earlier ('92) for Amphiuma. The cæcilians, as has long been known (Wiedersheim '79), have the olfactorius leaving the brain by two strands and these pass through separate foramina in the ethmoid so as to reach the nasal capsule. Details of the relations of the glomeruli are not abundant. In Ichthyophis (Burckhardt, '91) the glomeruli are included in the mass of the cerebrum and such is apparently the case in Salamandrina (Lee, '93, fig. 7). In Triton, on the other hand, a lobus olfactorius is developed, and the glomerular region is within the nasal capsule. (Burckhardt, '91.)

THE OPTIC NERVE.

This nerve presents few features calling for remark. In the latest stage studied the decussation of fibres has not taken place and the floor of the third ventricle is produced on either side, a reminiscence of the method of formation of the optic outgrowth, but the lumen in the nerve has entirely disappeared, (fig. 18).

EYE-MUSCLE NERVES.

Careful search with the higher powers of the microscope has failed to reveal any of the eye-muscle nerves except the third, the oculomotorius, and this was not successfully traced in detail. This nerve arises from the lower surface of the anterior part of medulla oblongata and then passes upwards, outwards and forward, its inter-cranial course being close to the parasphenoid. Finally it leaves the cranium by its own foramen which, in the earlier stages is through the trabecular cartilage; in the later through the bone. This foramen was supposed by Hay ('90)

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to be that for this nerve, although he did not find the nerve itself. In the foramen the nerve divides into two rami. The upper ramus passes above the ophthalmicus to innervate the superior rectus, and, as far as I could make out, nothing else. The lower ramus passes beneath the ophthalmicus profundus and soon becomes indistinguishable. I was unable to trace its fibres to the muscles, which, owing to the rudimentary condition of the eye, are greatly reduced.

In his discussion of the eye muscles and their nerves Allis ('95) has pointed out that the amphibia can be divided into two groups in the following manner, a division which is paralleled in the fishes (*sens. lat.*) In the first the superior ramus innervates the superior and internal rectus muscles. To this group belong the urodeles (and the elasmobranchs and dipnoi). In the second group, which contains the anura (and the ganoids and teleosts) only the superior rectus is innervated by the superior ramus of the oculomotor. In Ichthyophis, according to Allis, the relations of this nerve are as in the anura. For this reason I regret my inability fully to settle the matter for Amphiuma, as the point is one of some weight in deciding the affinities of Amphiuma and the cæcilians.

TRIGEMINALIS NERVE.

From the lower external angle of the medulla oblongata arises a thick root for the fifth nerve* in which are to be distinguished three bundles of fibres (fig. 16); a small bundle above, one of about the same size below, and a third, larger than the other two, lying between them. Of these the middle is continuous with the ascending tract of the fifth. The cerebral origin of the others was not traced, The fibres of the lower bundle are slightly larger than the others. Since Strong ('95) allows only general cutaneous and motor fibres to the fifth nerve, the conditions in Amphiuma are interesting and deserve detailed study on better material. These bundles pass forward, inside the

*I said ('92, p. 67) "I am unable to say how many roots the [fifth] nerve has as it comes from the brain. Several distinct groups of fibres go from the anterior angle of the medulla to the Gasserian ganglion." Referring to this Davison says ('05 p. 410) "Kingsley failed to find the roots of the fifth nerve. My sections show but one root," a construction considerably different from my actual statement.

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cranial cavity, just beneath and parallel to the anterior end of the facial ganglion, and enter the Gasserian ganglion. It was not found practicable to trace these elements farther than this point, except to see that some of the fibres of the middle bundle enter the mandibular ramus.

The Gasserian ganglion is somewhat lenticular in shape, concave internally and with its lower border considerably nearer the middle line than is the superior, the latter lying just beneath the ophthalmicus superficialis branch of the facial nerve. The whole ganglion is situated in the cranial cavity and lies in a recess bounded by the otic capsule and the various processes of the trabeculæ. I have been unable to ascertain whether there is any exchange of fibres within the ganglion between the ophthalmicus superficialis and the fifth. From the Gasserian ganglion arise the three main trunks of the fifth nerve.

RAMUS MANDIBULARIS. This is the most posterior and the most external in its point of exit from the Gasserian ganglion, and it is to be noted that there is no maxillaris nerve dividing later into maxillaris superior and mandibular rami but that these two branches are distinct from the first. The mandibularis leaves the cranium through its own foramen, bounded behind by the otic capsule, by the ascending process of the quadrate below, and above by the oto-trabecular bar.

Immediately after leaving the cranium the mandibularis gives off a small twig (*mas*[1]) which passes upward and forward into the masseter muscle, while a second and larger nerve (*temp*), passes forward, at first through the loose connective tissue outside the cranium, then beneath the ramus maxillaris superior to the outer side of the temporalis muscle.

The main trunk of the mandibularis passes outward, in front of and beneath the masseter muscle, sending from its dorsal surface a larger nerve (*mas*[2]) which passes upward and outward —paralleling, in projection, the main trunk—to the anterior portion of the masseter. Another twig (*so*), running directly outward, continues in this direction as far as the ramus mandibularis facialis externus and there divides, sending smaller twigs upwards and downwards to the skin. These apparently go to the

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adjacent sense organs but certainty on this point was not reached. Such a distribution is without parallel so far as I am aware.

The trunk of the mandibularis continues outwards to the upper margin of the lower jaw which it enters through the inferior dental foramen, and, passing between Meckel's cartilage and the dentary bone, divides into an upper and outer (mental) and an inner lower (mandibular) nerve.

The mentalis runs along parallel to Meckel's cartilage, finally entering its own canal in the dentary bone, just before which it gives off an inner branch (not shown in the diagram) which follows along the cartilage, sending off fine twigs to innervate the teeth. The main mentalis passes forward, then out through the mental foramen and finally breaks up to supply the skin of the anterior part of the lower lip. I noticed no anastomoses between the mentalis and the facial.

The mandibularis, after the separation of the mentalis, passes downward on the outer side of Meckel's cartilage, and then out of the jaw in the gap between the dentary and angulo-splenial bones. It now passes on the outer surface of the mylohyoid muscle, almost immediately dividing into two branches (not shown in the projection) the inner of which supplies the skin posteriorly, while the other continues forward without division, until in front of the angle of the mouth, it divides to supply the skin of the lower side of the lower jaw.

RAMUS MAXILLARIS SUPERIOR. This nerve is clearly a double one. It has in it fibres from both the Gasserian ganglion and from the dorsal (ophthalmicus superficialis) root of the seventh nerve. Hence it equals not only the maxillaris superior but the buccalis as well. The trigeminal portion arises from the dorsal crest of the Gasserian ganglion just below the place where ophthalmicus rests upon it (see account of this nerve in the section on the facialis). From this point this nerve passes out of the skull together with the ophthalmicus superficialis in a common foramen* and the two nerves remain in close connexion

*In the preosseous condition of the skull these nerves leave through the same foramen as does the mandidularis, but with the formation of bone the ramus mandibularis becomes separated from the others by a bony process, and the rest of the primary foramen is occluded by membrane.

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with each other for some distance. Still in transverse sections the two parts can readily be distinguished, the larger, facial element is above, the lower trigeminal portion being much smaller. These nerves at first follow closely the outline of the skull, lying in the angle bounded internally by the trabecula, above by the prootic and parietal bones, and externally by the masseter muscle. From this position they pass outwards, behind the tendon of the temporalis and between this and the masseter. Here the two nerves separate, and the course of the ophthalmicus will be followed in connexion with the facialis.

The maxillaris now sends off an upper branch (5) the first of the maxillaris (buccalis) branches, a blood vessel (fig. 8) coming between the two nerves. The branch almost immediately gives off small twigs to the adjacent sense organs, but its main portion passes to the outside of the blood vessel, and then beneath the outer hinder surface of the eye, sending a twig downward to the upper lip and then dividing up into small twigs to supply the suborbital line of sense organs.

The main trunk of the maxillaris superior passes forward, nearly parallel to the external surface of the head, running below the eye (fig. 6), giving off, just behind that organ a small ramulus which was lost in the connective tissue, and which may possibly be the abducens nerve, which otherwise could not be found. Beneath the eye and at about the midddle of the orbit the maxillaris gives off a second (buccalis) branch (4) which, like the one already mentioned, goes to the suborbital sense organs.

At the level of the anterior margin of the orbit the main trunk of the maxillaris divides into three rami; outer (3), middle (2) and inner (1). The outer of these immediately passes through a foramen in the maxillary bone and soon breaks up into fine twigs supplying the sides of the head just above the upper lip. The middle branch (2) almost immediately fuses (fig. 5) with a branch of the ophthalmicus profundus as has been described by H. H. Wilder ('92). At this point the compound nerve (nasalis externus), passes through the same foramen in the maxillary bone* as branch 3. It then continues forward in a

*Apparently this is the foramen to which Cope refers ('66, p. 105) as being similar to the tentacular foramen in certain cæcilians, and as indicating close affinities with that group.

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groove on the outer side of the maxillary and later turns outward and forwards to supply the sense organs of the skin in front of those reached by branch 3. The inner branch (1) likewise fuses with a second branch of the profundus and the common trunk thus formed (the ramus glandularis I, of Wilder) enters the nasal capsule from behind, and passes forward, outside of and below the posterior olfactory diverticulum. In front of this structure it runs more to the exterior, between the cartilaginous nasal capsule and the maxillary bone. Then by an oblique foramen it passes through this bone and immediately breaks up into twigs innervating the sense organs at the tip of the snout.

RAMUS OPHTHALMICUS PROFUNDUS. This trunk arises from the anterior extremity of the Gasserian ganglion and leaves the cranial cavity by its own foramen near the floor of the skull. This foramen is bounded above by the ascending process of the the quadrate, below by the trabecula and the pterygoid cartilage. Outside the skull the nerve runs close to the cranial wall, and at first between it and the temporalis muscle. It gives off no branches until at the plane of the posterior surface of the nasal capsule it divides into upper (nasalis internus) and lower ramuli, the lower portion dividing again into inner and outer branches.

The upper division, the nasalis internus (*nas. int.*) follows along the cranial wall, passing above the rectus muscles, and enters the nasal capsule, where it passes just above the olfactory nerve to the inside of the nasal epithelium. In its course from its origin from the main trunk of the profundus it gives off a few twigs, the first of which* (*eth. c.*) passes upward and forward, between the eye and the cranium until it reaches the level of the ophthalmicus superficialis where it divides into two branches, inner and outer. The inner of these goes upward and forward, passing through the process of the frontal bone which articulates with the prefrontal; then between frontal and prefrontal to the top of the head, where it divides, one branch going obliquely toward the median line and the other forward, both running immediately beneath the skin, which they innervate. The outer branch curves outward, first passing over the ophthalmicus

*In order to avoid confusion in the plat of the nerves, this twig is shown projected on the right side of the diagram while the nasalis internus from which it arises is represented on the left.

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superficialis, and then through the margin of the prefrontal, dividing inside this bone into two twigs which leave the prefrontal by separate foramina, to innervate the skin lying immediately above. This nerve (*eth. c.*) which in origin, but not in distribution seems to resemble the ethmoideus caudalis of mammals, was apparently first noticed by Fischer ('64, p. 130) in Necturus, and has since been seen by several other students in both anura and urodeles. No ciliary nerve was found in Amphiuma.

In front of this nerve, (which for want of a better name I have called the ethmoideus caudalis) is a small nerve (θ) arising from the same trunk (nasalis internus) which passes upward to break up in the connective tissue between the olfactory epithelium and the cartilage wall of the capsule above. Just in front of this, a smaller twig (not figured) passes downwards to the inner side of the olfactory capsule.

The main branch of the nasalis internus continues forward inside the nasal capsule and close to the vertical lamina of the premaxillary, sending off twigs which run among and become confused with the branches of the olfactorius but without, so far as I could see, anastomosing with them. Some of these twigs appeared as if distributed to the capillaries of this region. Near the front of the head the nasalis internus divides into dorsal and ventral branches which continue forward to the tip of the snout.

The outer and larger division of the lower half of the profundus must retain the name. It lies just medial to and beneath the eye and at a lower level than the other two (*oph. prof* *). At about the plane of the origin of the oblique muscles of the eye it gives off from its dorsal surface a nerve, the ramus glandularis II of Wilder (α) which runs horizontally forward, enters the dorsal portion of the nasal capsule from behind, and bending upward, passes through the dorsal cartilage of the nasal capsule and then out between the nasal and maxillary bones. It then breaks up into fine twigs, apparently innervating the glands (glandulæ laterales) just above and outside the nasal capsule. Wilder ('92) studying older specimens has traced the main trunk of this nerve forward to the tip of the snout, but I could not do this.

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The rest of the ophthalmicus profundus, after giving off this glandularis II almost immediately divides, its two branches uniting with the middle and inner divisions of the maxillaris superior; their subsequent course has been described above.

The inner component of the lower half of the profundus (*rcp*) forms the commissure between the profundus and the ramus palatinus of the seventh. Its further course is described in connexion with that nerve.

The foregoing may be summarized as follows: The trigeminal has motor and general cutaneous fibres; it divides into three main trunks as it leaves the Gasserian ganglion. Besides these truly trigeminal components it receives facial elements in a branch from the lateralis of the seventh nerve which pass into maxillaris superior, which therefore must be regarded as a compound of the maxillaris superior proper and buccalis rami of piscine ichthyopsida.

The branches of the trigeminal form anastomoses with each other and with the nerves as follows: (1) two branches of the ophthalmicus profundus with two of the maxillaris superior. (In recent papers this condition has been described, among amphibia, only in Amphiuma. In higher vertebrates this union, or a similar one between maxillaris and lachrymal, is common). (2) A branch of the ophthalmicus profundus and the palatine branch of the facialis. Other connexions between the nerves were not found, possibly owing to the young stage of the specimens studied. Further discussion will follow the account of the seventh and eighth nerves.

ACUSTICO-FACIALIS NERVES.

This nerve-complex arises by two roots, about equal in size, placed the one directly over the other. The more dorsal of the two is the lateralis root of the seventh (the VIIb of Strong's earlier papers). The ventral root shows two portions; an upper, which is largely auditory, and a lower which contains facial components. It was found impossible to say positively that either of these portions were either entirely facial or entirely auditory, nor was it possible to trace their cerebral origins beyond a doubt. Some of the fibres of the ventral component

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could be traced inwards to near the posterior longitudinal fasciculus but absolute continuity could not be demonstrated. Almost immediately after leaving the brain the lower half of the acustico-facialis divides into two portions; one posterior and purely acustic in function, the other containing both elements.

ACUSTICUS. The acusticus root, as soon as it leaves the brain, enters the auditory ganglion which has a flattened lenticular outline and lies outside and a little below the facial portion of the nerve. From it arises the posterior acustic nerve mentioned in the preceding paragraph. This runs backwards, carrying with it on its lower surface some of the ganglion cells, and enters the otic capsule by its own foramen, some of the ganglion cells being situated in this opening. From this ganglion arise several branches as follows:

(1) The ramus lagenæ (*lag.*) which arises from the lower surface of the ganglion, and runs downwards and backwards, passing in front of and below the ductus perilymphaticus and thence to the macula lagenæ.

(2) The ramus neglectus (*neg.*) which arises from the upper portion of the ganglion, runs upward in front of the perilymphatic duct and then coming behind it, passes inwards to the macula neglecta.

(3) The ramus ampullæ posterioris (*amp. post.*) arises beside the r. neglectus, gradually sinks to the floor of the otic capsule, and then follows along the lower surface of the posterior semicircular canal, finally curving upwards and outwards to the ampullar region.

(4) The posterior ramus sacculi (sac^2) arises from the anterior division of the auditory ganglion, opposite the origin of the VII-VIII from the medulla. It is a small twig which branches inside the cranial cavity into two branches (only one figured) passing through the osseous wall of the capsule by separate foramina and thence to the sacculus.

(5) The anterior ramus sacculi (sac^1) arises just in front of the last, from the lower part of the auditory ganglion, enters the otic capsule by its own foramen, and then curves backwards, supplying the medial wall of the sacculus just in front of the region innervated by the other sacculus twigs.

In the earlier (preosseous) stages all of the auditory rami so

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far mentioned pass through a common foramen in the chondrocranium in order to reach the sensory epithelium, but with the appearance of bone separate foramina are found. Again, in the earlier stages the line of division between the two main groups of auditory nerves corresponds to this foraminal grouping, a fact which accords well with some of the views of Ayers ('91, '92) upon the compound nature of the ear.

The main body of the ganglion acustici, triangular in outline whether viewed from in front or from above, lies in the angle between the anterior wall of the otic capsule and the trabecular floor of the cranial cavity, the ganglion lying entirely within the cranial walls. The fibres of the anterior division of the acusticus arise from the upper surface of the ganglion and pass into the otic capsule by a single foramen immediately above that for the exit of the facialis from the skull. This anterior division of the auditory nerve runs at first directly outwards and gives off the following branches:—

(1) The ramus ampullæ anterioris (*amp. ant.*) which goes forwards and outwards, reaching the sensory epithelium of the ampulla from the lower outer side.

(2) A short ramus utriculus (*utr.*) which arises from the posterior side of the main trunk, supplying the macula utriculi.

(3) The ramus ampullæ exterioris (*amp. ext.*) which follows the ventral surface of the external semicircular canal, dividing at the tip to innervate both sides of the ampullar sense organ.

FACIALIS. As was noted above there are two divisions to the root of this nerve, one giving rise to the lateralis components, the other—closely connected with the auditory nerve—carrying motor and fasciculus communis fibres.

Upon its emergence from the medulla the lateralis trunk goes straight forward inside the cranial cavity and becomes compressed to a ribbon-like structure between the brain and the wall of the otic capsule. In this region is the ganglion which extends forward as far as the combined auditory and geniculate ganglia. Here the lateralis divides, the upper portion continuing straight forward as the ophthalmicus superficialis while the lower half unites with the ventral root of the seventh, later to emerge as the lateral-line component of the nerve, going to the lower jaw, the distribution of which will be traced later.

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The ophthalmicus superficialis contains at first buccalis fibres. It passes directly forwards over the top of the Gasserian ganglion and leaves the skull in company with the maxillaris superior, the lateralis components in the compound trunk thus formed being easily recognized by their larger size. The separation between the ophthalmicus and the maxillaris superior occurs just behind the eye. The ophthalmicus passes upwards above the eye, then moves to its upper inner position beneath the projecting prefrontal bone (fig. 6) and in this way enters the osseous nasal capsule, but remains outside the cartilage walls (fig. 5). So far in its course it has given off few fibres which pass dorsally to innervate the overlying sense organs. Farther in front it branches more abundantly and winds its way forward, the twigs passing sometimes inside, sometimes outside the cartilage bars which make up the nasal basket. Its last fibres can be traced to the very tip of the snout.

The buccalis cannot be recognized as a branch distinct from the maxillaris superior and has been described in connexion with that nerve.

The lower half of the lateralis trunk passes downwards and joins the other (motor and fasciculus communis) portions of the facial and leaves the skull along with the hyomandibular trunk, later separates as the mandibularis facialis externus, the course of which will be followed below.

In the lower root of the seventh I could not distinguish the two roots "VIIaa VIIab" of Strong, but it was easy to follow the common trunk through the acustico-facialis complex until it emerged as the hyomandibularis nerve. In this passage it could readily be seen that it was accompanied by lateralis fibres. I could distinguish no palatine ganglion but palatine and mandibular fibres passed out from a common glanglionic mass.

The ramus hyomandibularis passes directly outwards from the skull, immediately below the anterior division of the acusticus. Its course is almost horizontal and it gradually curves backward, below and to the outside of the otic capsule. Here it passes, first, along the inner surface of the stapedial process of the quadrate, then along its lower surface to a point just in front of the articulation of the quadrate with stapes. Here the

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main trunk gives off several branches in close proximity with each other.

Of these the first is the alveolaris nerve which at first runs downwards and then forwards, lateral to the ceratohyal cartilage and the lateral angle of the buccal cavity, and finally enters, by means of an elongate foramen, into a canal lying in the angulosplenial bone below the Meckelian cartilage, in which it can be traced far forward in the jaw. Fischer could not assure himself of the existence of this nerve in Amphiuma but apparently the nerve here described is the same as that which he calls by the same name ('64, p. 133) in Siredon, as well as the alveolaris of von Plessin and Rabinowicz in Salamandra ('91) and that of Herrick in Amblystoma. It is to be noted that I have seen none of the twigs mentioned by Herrick ('94, p. 194) as running to the gums nor have I found any commissure between this nerve and the mentalis branch of the fifth. It might be said that the name alveolaris is not well chosen, so far as Amphiuma is concerned, since in this animal it has no relation to the alveolar groove which lies some distance above it.

The ramus mandibularis facialis externus, the sensory element of the lower jaw, leaves the hyomandibular trunk close to the origin of the alveolaris. It curves under the stapedial process, (fig. 17) runs along its lower surface and then between the stapedial and the digastric muscle, soon giving off from its upper surface a branch (δ) which runs forwards, upwards, and outwards between the digastric and the masseter muscles and soon divides into a number of twigs supplying the adjacent sense organs. The main nerve continues forwards, outwards, and downwards, at first between the paraquadrate bone and the digastric muscle and then along the outer angle of the lower jaw, just beneath the skin, giving off twigs to the sense organs of the lower lip in its course. It hardly needs to be said that this is the nerve called buccalis by von Plessin and Rabinowicz and by Herrick. The true buccalis is however a nerve of the upper jaw.

A little beyond the point where the mandibularis facialis externus leaves the hyomandibular is the origin of the large trunk of the hyomandibularis accessorius. This is given off from the lower surface of the hyomandibular and passes outwards.

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and downwards to the outer surface of the mylohyoid muscle, (fig. 17) between which and the skin it runs for the rest of its course. At about the level of the articulation of the quadrate and the lower jaw it divides into inner and outer branches (*hm*^{i} and *hm*^{e}) which run, with slightly diverging courses, toward the tip of the jaw. Beneath the eye the outer branch receives a twig from the mandibular branch of the fifth and from this point the two run forward as a common nerve. Herrick has noticed a similar commissure in Amblystoma and is of the opinion that this lends additional probability to the view that this nerve is the homologue of the chorda tympani, a view which I am not disposed to dispute.

A little behind the origin of the accessory hyomandibular is that of the true hyomandibular (*hm*) which passes downwards from the ventral side of the main trunk and almost immediately divides into two rami distributed the one anteriorly the other posteriorly. The anterior branch (*hm*^{1}) goes downwards and forwards to the anterior belly of the digastric muscle where it breaks up in fine twigs. The posterior division (*hm*^{2}) runs downwards and backwards along the ventral surface of the mylohyoid muscle.

Just back of the separation of the hyomandibularis the main trunk divides into three nerves; Jacobson's commissure between the glossopharyngeal and the facial, a nerve to supply the digastric muscle, and a third for the dorsotrachealis muscle.

Jacobson's commissure (ramus communicans cum glossopharyngii—Comm. VII+IX) curves around the outer wall of the otic capsule, then around the fourth efferent branchial artery and then bends inwards to meet the main glossopharyngeal nerve in connexion with which it enters the glossopharyngeal ganglion. No attempt has been made to trace the origin or distribution of the fibres in this commissure. On *a priori* grounds one must regard it as a branch of the ninth nerve but I cannot say whether its fibres belong to the somatic sensory, lateral line or visceral sensory system (*Cf.* Cole '98 pp. 145-148.)

The digastric branch (*dig*) at once enters the digastric muscle in company with the nerve to the dorsotrachealis. It breaks up almost immediately into fine twigs which are soon lost among the muscle fibres.

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The nerve to the dorsotrachealis muscle (*dtr*) passes outwards and gradually backwards through the digastric to the lower posterior margin of the muscle, which it follows backwards to the anterior end of the thymus gland. It crosses the outer surface of the thymus, gradually rising in its course, and curving around the posterior margin of the gland, enters the upper posterior portion of the dorsotrachealis muscle. So far as I am aware this nerve has been seen only in Amphiuma by Fischer ('64 p 136) and my observations agree closely with his except where he says "Es giebt nur einen schwachen Faden an dem ihm benachbart verlaufenden Hauptstamm des Vagus," for I find in my sections no trace of such a connexion. Fischer farther says that it is distributed to the hyotrachealis muscle but I did not trace it so far.

The ramus palatinus (*pal*) arises from the lower surface of the facial ganglion and passes directly downwards through the floor of the skull and then forward between the trabecular cartilage and the edge of the parasphenoid. Later it continues forward in the same direction between the margin of the parasphenoid and the quadrate, immediately above the external jugular vein, (fig. 20). Farther forwards it runs in the angle between the pterygopalatine cartilage, the trabecular and the parasphenoid as far as the palatopterygoid extends. Then it follows along the suture between parasphenoid and orbitosphenoid until the antorbital process is reached. It passes beneath this process and turns upwards, dividing into two branches, one of which continues upwards to unite with a branch from the ophthalmicus profundus nerve, while the other runs inwards and forwards inside the nasal capsule between the nasal epithelium and the capsular wall. Here it gradually descends to the floor, gradually dividing into twigs which become lost in the connective tissue of that region.

The other branch (ϵ), containing both palatine and profundus constituents, passes forwards from the junction of its component nerves, just above the antorbital process to its tip. It then bends around the proximal end of the olfactory organ, goes downward, passes between the maxillary and palatine bones and thence forward upon the roof of the mouth.

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According to Coghill ('01) both the palatine and the ophthalmicus profundus divide, in Amblystoma, and fibres from both occur not only in the nerve here called ϵ but in that here called palatine which passes to the inner side of the nasal capsule. My slides do not allow me to settle the matter for Amphiuma.

I find no trace of a palatinus caudalis like that described by Herrick in Amblystoma nor of a palatinus caudalis like that described by Pinkus ('94) in Protopterus, which according to that author is the same as the "alveolaris" found by Wilder ('91) in Siren.

VAGUS-GLOSSOPHARYNGEUS GROUP.

In Amphiuma, as in the Amphibia generally, the vagus and the glossopharyngeus nerves are closely associated with each other, and I have been unable, in all cases to trace the different components through the ganglion. For the compound ganglion five roots are readily distinguished, this number is constant, so far as published observations go, for the whole of the Amphibia. The first or most anterior of these (fig. 21) is triple as it arises from the medulla. The dorsal and middle components of the root are about equal in size, the ventral much smaller. All three are nearly in the same vertical plane and are so close to each other that their distinctness can only be recognized by the microscope. All three unite into a common trunk, the components of which can be traced about half way back to the ganglion. The trunk runs backwards, inside of the cranial cavity until it joins with the second vagus-glossopharyngeal root which is single and arises from the extreme lateral part of the medulla, and is immediately followed by the third root, more dorsal in position. Considerably farther back are the two remaining roots, the fibres of which unite with a common trunk which runs forward to enter the ganglion.

From its position the most anterior of these five roots would naturally be regarded as glossopharyngeal in its nature and so it has been by all authors before Strong. In Amphiuma I have traced a bundle of fibres from this root through the vagus-glossopharyngeal ganglion into the nerves which below I have designated as the superior and inferior rami of the vagus. From this it would follow that the root in question is in part if not

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wholly vagus in its nature. I was not successful in tracing fibres from the other roots.

The vagus-glossopharyngeal ganglion is the largest of the cranial ganglia. Its outline, as seen from above, is shown in the general scheme of the nerves. In transverse section it is oval behind, but in front it is deeply excavate above to accommodate the posterior end of the otic capsule. It lies entirely without the cranial walls and the nerves arising from it take their origin from its upper outer margin, (fig. 15).

The trunk which arises from the anterior outer portion of the ganglion must be regarded as glossopharyngeal in its nature. Its fibres arise from the ganglion cells and I could not trace any of them back into the cranial roots. In other words this nerve is apparently wholly sensory in its origin, a fact which is in full accord with its distribution in Amphiuma, for none of its branches were traced into muscles. This nerve passes upwards and forwards around the hinder edge of the otic capsule and soon divides into inner and outer branches. The outer, which is the commissure of Jacobson already referred to, passes above the external carotid artery, then over the dorsal edge of the posterior mylohyoid muscle to unite with the hyomandibularis as already described.

The inner branch—the true glossopharyngeus—passes between the external carotid and the jugular and then divides into hyoid (*gph*) and pharyngeal (*gpp*) branches. The pharyngeal division goes forwards and inwards in the loose connective tissue above the pharynx and there breaks up into fine twigs, which apparently innervate the sensory epithelium of the dorsal wall of the pharynx. The hyoid division pursues a more direct course forwards and downwards until it reaches the upper surface of the hyoid cartilage along which it courses forwards. It was not traced to its tip. This branch may be the lingualis of authors (which otherwise is not present) but since it differs considerably from the lingualis in its origin and early course, and since it was not traced into the tongue, it has been called by this non-committal name.

From the posterior surface of the main glossopharyngeal trunk arises a small nerve (λ) which in all its details, so far as

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followed, is the supratemporalis of authors. It passes outwards and upwards around the lower edge of the longissimus dorsi muscle and then inwards and slightly backwards towards the middle line. Its twigs were not traced to their termination, but in all probability they go to the sense organs in the occipital region. Fischer failed to find this nerve in the urodeles which he studied unless it be a branch figured without reference in Necturus ('64, pl. III[a]). It is not mentioned in Diemyctylus by Mrs. Gage ('93), by Fish ('95) in Desmognathus, nor by C. J. Herrick ('94) in Amblystoma, unless it be included in his "group 4" of vagus nerves. In Necturus Kingsbury ('95) does not specifically mention it, although he recognizes the existence of lateralis fibres in the glossopharyngeal. On the other hand von Plessin and Rabinowicz ('91) find it (p. 18, no. 1) in Salamandra, and Miss Bowers ('00) distinctly recognizes it in Spelerpes.

The supratemporalis nerve possesses considerable interest from its relations. Without any exhaustive study of the literature, the following references to its existence have been found. Its existence is certain selachians has been known since the days of Stannius ('49, p. 79, there called ramus dorsalis). In the ganoids it has been described by Allis ('89) in Amia, by Goronowitsch ('88) in Acipenser and by Pollard ('91) in Polypterus. In all of these it emerges from the brain in connexion with the glossopharyngeal, although its deeper origin must be, as Allis points out ('97, p. 746) for Amia, from the lateralis tracts. In Polyodon apparently (Collinge, '94, p. 519, pl. 40, fig. 11 l') the same nerve is connected with the vagus. In those teleosts where it has been found as in Gadus (Cole, '98) Batrachus (Miss Clapp, '99) and various siluroids* (Pollard, '93) it arises as in Polyodon. In the limited literature upon the Dipnoi I have found no reference to a corresponding nerve; Pinkus in his elaborate paper ('94) on the cranial nerves of Protopterus does not mention any nerve that can be compared with it. Neither do I find in either of my specimens of Protopterus a correspond-

*In the siluroids there is an interesting connexion of this nerve with the recurrent facial (*cf.* Allis, '97, p. 628 and Cole, '98, p. 167). C. J. Herrick, '99, failed to find this nerve in Menidia.

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ing set of sense organs, nor is any described by or figured by Wiedersheim ('80) W. N. Parker ('92) or Kingsbury ('95). In the anura Strong describes ('95, p. 144) a supratemporalis nerve in the tadpole. This passes out in the common vagus-glossopharyngeus trunk and then passes forward upon the sides of the head, but its homology with the supratemporalis in the other forms mentioned is not beyond a doubt.

The fact that the supratemporalis of the urodeles agrees closely with that of the ganoids is of considerable interest when taken in connexion with the different relations in the teleosts, these showing that the nerve—while lateralis in nature—is variable in its associations and that the urodele condition is derivable from that found in the ganoids. In this connexion the apparent absence of a corresponding nerve in the Dipnoi is suggestive.

Just behind the vagus trunk which has just been described, is the branchial trunk of the same nerve. Just after its emergence from the ganglion it gives off, above and in front, a motor branch (*p. dig*) which courses at first upwards and outwards until it reaches the outer edge of the longissimus dorsi; then it runs forwards between this muscle and the posterior digastric, and finally enters the latter muscle to innervate it. The main trunk (br^1) is the first branchial nerve. It runs outwards and slightly backwards until it reaches the upper surface of the first epibranchial, and then turns inwards and forwards along the outer surface of this cartilage. In this as in the other branchial nerves no division was noticed into pre- and post-trematic branches.

The second and third branchial nerves (br^2 and br^3) leave the ganglion by a common trunk (not indicated in the plan as distinct from the ganglion.) This trunk runs backwards a short distance and then divides into the two branchial nerves. These pass to the corresponding gill arches much as described for the first branchial. The third of these gives off just before reaching the branchial arch a small twig (not figured) which runs backwards in the loose tissue; and besides, after reaching the outer surface of the cartilage, it gives off a second branch which extends outwards until it reaches the nerve to the dorsotrachealis

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muscle described above. It passes below this nerve, just touching it in its course, until it reaches the fourth efferent branchial artery, at about the level of the anterior end of the thyroid. It follows this vessel until it turns inward to join the radix aortæ. It is possible that this is the nerve described by Fischer ('64) as connecting the dorsotrachealis branch of the facialis within the tenth nerve. So far as I am aware no similar nerve has been described in any Amphibian.

Three large trunks arise from the hinder end of the vagus-glossopharyngeal ganglion and run backwards in a direction nearly parallel with the axis of the body. Since I have not traced these to their termination and hence am not certain of their homologies they are referred to according to their position as they leave the ganglion, as superior, median, and inferior, a course which will lend to no confusion.

The median branch (*x.m.*) runs back into the longissimus dorsi muscle in which it could be traced as far backwards as the level of the shoulder girdle (as far as the series of sections extended). At its origin it occupies a position between the other two vagus trunks, but farther back it arises above the others and occupies the most dorsal position. The superior nerve (*x. s.*) runs in a similar manner beneath the longissimus dorsi muscle, and farther back between this and the intertransversales muscles. Neither median or superior nerves, so far as traced, give off nerves to other structures nor connect with other nerves.

The inferior nerve (*x. inf.*) runs at a lower level, just median to the dorsotrachealis muscle, to its anastomosis with the hypoglossal nerve.

HYPOGLOSSAL NERVE.

The hypoglossal arises by four roots, two dorsal and two ventral which immediately unite into a common trunk to pass through the intervertebral spaces by a single foramen. Outside the vertebral region is the lenticular hypoglossal ganglion. That these are true dorsal and ventral roots is shown not only by their origin but by the course of the corresponding nerves through the ganglion, the ventral roots being readily traced

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through the ganglion beneath the ganglion cells which occupy the dorsal portion only of the ganglionic enlargement.

Besides several minute twigs, several small nerves (*lon. d.*[1]) arise from the ganglionic enlargement in front of the ganglion cells and pass dorsally into the longissimus dorsi muscle. The main hypoglossal trunk arises from the posterior end of the ganglion, some of its fibres being of ganglionic origin and some traceable directly from motor roots. The nerve runs obliquely backwards and outwards between the longissimus colli and rectus capitis anticus muscles, soon sending a twig (*r. cap.*) into the latter. A little behind this is a second nerve (*lon. d.*[2]) which comes in contact with the superior division of the vagus (supra) and then passes around the lateral margin of the longissimus dorsi and then upwards and inwards through this muscle, some of the twigs extending to the dorsal surface of the body and some lying close to the vertebræ.

The main trunk of the hypoglossal (*hyp*) continues back in the longissimus colli, nearly parallel with the superior division of the vagus, to its fusion with the inferior branch as already noticed. From this union arise nerves which supply the cucularis (*n. cuc*) and dorsotrachealis (*d. tr*) muscles, the inner side of the first afferent branchial artery (*af. br*[1]) as well as the main hypoglossal trunk. This latter passes at first downwards to reach the outer surface of the sterno-hyoid muscle, its course taking it behind the dilator tracheæ. It follows along the outer margin of the sterno-hyoid until it reaches the glossohyoid in which it runs to the anterior branch of the hyoid cartilages.

The conditions presented by the hypoglossal are of considerable interest. The recent discussions of this nerve in Ichthyopsidans have been so well summarized by Herrick ('99, p. 234 *et seq*) that only a few points need mention here. Of present interest is the fact that in the larval stages both dorsal and ventral roots occur and hence the nerve corresponds closely to to the pattern of a spinal nerve. In the account of von Plessin and Rabinowicz a ganglion of the dorsal root is described in Salamandra but the root in the stages studied by them (2½-3 cm. long) had lost its connexion with the spinal cord. In my earlier paper ('92) I pointed out the existence of this gan-

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glionated root in Amphiuma. Mrs. Gage ('93) and Miss Bowers ('00) find somewhat similar conditions in Diemyctylus and Spelerpes respectively. On the other hand Fish ('95) in Desmognathus and Kingsbury ('95) in Necturus find only ventral roots. The same may be said of Amblystoma as described by Herrick ('94.) In regard to this last genus I may say that in the young of both *Amblystoma punctatum* and *A. jeffersonianum* I find dorsal ganglionated roots, but in Siredon-like larvæ of the former species, 45 mm. long, only the two ventral roots can be found and the ganglion has disappeared. As Herrick studied larvæ 8 to 10 cm. long the discrepancy is easily explained.

Another point of interest is the existence of two pairs of roots for this nerve in Amphiuma and young Amblystomæ, suggesting that we have to do here with a double nerve such as has been described by Weidersheim ('80) and Pinkus in Protopterus where also dorsal roots occur. Burckhardt ('82) notes only ventral roots in this form, with in one instance an interesting case of shifting of roots. In the ganoids there is no distinctively hypoglossal nerve, but in Polypterus (Pollard '92) and in Amia (Allis '97) the nerve which goes to the branchio-mandibular muscle is apparently homologous with the hypoglossal nerve and this has a multiple origin with ganglia on one or both the dorsal roots.

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EXPLANATION OF PLATES.

REFERENCE LETTERS.

Alv, alveolaris nerve.
AfBr, nerve to afferent branchial vessel.
Ags, angulo-splenial bone.
Amp, nerve to posterior ampulla.
Amp. Ant. Ext. Post, nerves to ampullae of semicircular canals.
α branch of Ophth profundus.
AO, antorbital cartilage.
Art. articular bone.
R1-4, nerves to branchial arches.
BrPl, brachial plexus.
BV blood vessel.
CB, cerebral lobes.
ChP, choroid plexus.
Chy, ceratohyal.
Com vii+ix. commissure (Jacobson's) between facialis and glossopharyngeal nerves.
δ See p. 306.
Dent, dentary bone.
Dig, digastric muscle and nerve to same.
DigA and P, anterior and posterior divisions of digastric muscle.
DiN, nerve to digastric muscle.
DrV, dorsal root of fifth nerve.
Dtr, nerves to dorsotrachealis muscle.
ε See p. 308.
EB Ethmoid Plate.
EC external carotid.
EthC, nerve resembling the ethmo caudalis.
F, frontal bone.
GG, Gasserian ganglion.
GH, glossohyal muscle.
GlE, external nasal glands.
GlH, glossohyal muscle.
GlNIP nerves to glandulæ nasalis profundis.
GlNIS, nerves to glandulæ nasalis superiores.
GP, glossopharyngeal nerve.
GpA, glossopharyngeal, anterior portion.
GpP, glossopharyngeal, posterior portion.
HME, external branch of hyomandibular nerve.
HMI, internal branch of hyomandibular nerve.
Hyp, hypoglossal nerve.
HMA, accessory hyomandibular
JC, Jacobson's Commissure (commissure between VII and IX.)
JD, Jacobson's duct.
JG. Jacobson's gland.
λ, supratemporalis.
LA, levator arcuum muscle.
LB, levator bulbi.
Lag, nerve to lagena.
Lev, nerve to levator arcuum.
LonD, nerves to longissimus dorsi muscle.
Mand, mandibularis nerve.

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Mas, masseter muscle and nerve to same.
MasT, tendon of masseter muscle.
MaxSup, maxillaris superior nerve.
MC, Meckel's cartilage.
Med, medulla.
Ment, mentalis nerve.
MFE, maxillaris facialis externus nerve.
MH, mylohyoid muscle.
MHP, mylohyoid, posterior portion.
MrV, medial root of fifth nerve.
Mx, maxillary bone.
MxS, maxillaris superior nerve and its branches.
N, nasal bone.
Nas.In, nasalis internus nerve.
N.C, nasal capsule.
N.Cuc, nerve to cucularis muscle.
Neg, nerve to macula neglecta.
NI, nasalis externus nerve.
OcM, oculomotor nerve.
Olf, olfactory nerve.
OP.OphProf, ophthalmicus profundus nerve.
OPP, ophthalmicus profundus nerve.
OPS, ophthalmicus superficialis nerve.
OpSu, ophthalmicus superficialis nerve.
OS, orbitosphenoid bone.
P, parietal bone.
Pal, palatine nerve.
PDig, posterior digastric muscle and nerve to same.
Pf, prefrontal bone.
Pmx, premaxillary.
PQ paraquadrate.
Ps.,*Psph*, parasphenoid.
Pt, pterygoid bone.
Ptc, pterygoid cartilage.
Q, quadrate.
RcomO communicans between maxillaris superior and ophthalmicus profundus.
RcomP, communicans between ophthalmicus profundus and palatine.
RCap, nerve to rectus capitis muscle.
RInf, rectus inferior muscle.
RIX root of ninth nerve.
RV, root of fifth nerve.
R VII+VIII roots of seventh and eighth nerves.
Sac, nerve to sacculus.
SO, nerves to sense organs.
St, stapes.
StH. sternohyoid muscle.
Stp stapedial process.
Sp 1, *2*, first and second spinal nerves.
T, teeth.
Temp, temporalis muscle and its nerve.
θ See p. 301.
Utr, nerve to utriculus.
Vag. Gang, vagus ganglion.
VP, vomero-palatine.
V. R. V. ventral root of fifth nerve.

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XInf, *XM*, *XS*, inferior middle and superior rami of tenth nerve.

PLATE I.

Projection of cranial nerves of Amphiuma seen from above. In dotted outlines are shown the positions of the brain, nasal cavity and eye. The transverse dotted lines are drawn forty sections apart and show the locations of the sections figured upon the next plate. Fifth nerve lined, seventh dotted, second, eighth and twelfth black.

PLATE II.

Twelve transverse sections through the head of Amphiuma, illustrating the position of the nerves and their relations to other structures. For the planes of the section see the dotted lines on the preceding plate.

PLATE III.

Figure 15. Relations of ninth and tenth nerves at vagus ganglion.

Figure 16. Fibre tracts forming the root of the fifth.

Figure 17. Passage of nerve (θ) around stapedial process of quadrate.

Figure 18. Origin of optic nerve, showing lack of chiasma and persistence of rudiments of original cavity of optic stalk.

Figure 19. Origin of ventral root of hypoglossal nerve.

Figure 20. Longitudinal section showing origin of palatine from the ganglion of the seventh, and the absence of a distinct palatine ganglion.

Figure 21. Three sets of fibres forming the first root of the vagus nerve.

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THE SYSTEMATIC POSITION OF THE CÆCILIANS.*

By J. S. Kingsley.

Scarcely any question regarding the classification of the Amphibia possesses more interest than that of the position to be accorded to the Gymnophiona and Amphiuma. By the older writers they were regarded as remote from each other, Amphiuma being regarded as a member of the subclass Urodela, the blind worms constituting a distinct order variously termed Apoda, Gymnophiona, Cæciliæ, etc. In 1869 (p. 104) Cope first advanced the view that Amphiuma was the living representative of the group from which the gymnophiona have sprung. He maintained this in several subsequent papers even to the last ('95), and this view has been adopted by Hay, Ryder, Davison and others. The Sarasins in their monograph upon the Ceylonese blind worm have taken a different position. According to their view ('90 p. 241) Amphiuma must be grouped with the gymnophiona and can only be regarded as a permanent larval form of that group. The various authors who have written upon the subject have brought forward numerous points of similarity between these forms, but before accepting their conclusions the resemblances should be analyzed and a decision arrived at as to how far they can be utilized as a basis of taxonomy. These points of resemblance are :—

(I) The presence of scales in both Amphiuma and the gymnophiona (Cope '66 p. 105.

(II) The abbreviation of the lower jaw in the young (Davison '95 p. 406.

(III) The existence in both of an ethmoid bone lacking in other urodeles (Cope '86 p. 443 ; '89 p. 213.

(IV) "The free margin of the frontal bone [of Amphiuma] seems to foreshadow the over roofing of the orbit and temporal fossa seen in Cæcilia" (Cope '66, p. 105, '86 p. 442 ; '89 p. 214.

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* Studies from the Biological Laboratories of Tufts College No. XXX.

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V The presence, in both of amphicœlous vertebræ (Davison '95, p. 407.

VI The same prominent horizontal anterior inferior processes of the vertebral centra (Cope '66 p. 105; '86 p. 442. Two anteriorly directed hypapophyses of the precaudal vertebræ (Cope '86 p. 443.

VII The rudimentary appendages of Amphiuma, their complete absence in gymnophionia (Sarasins '90, p. 241.

VIII The discovery, by Strasser, of small cartilages in cæcilians in the positions of the elements of the scapular arch of urodeles (Cope '89 p. 222.

IX The existence in Amphiuma of "a canal passing through the o. maxillare from near the middle of the orbit, foreshadowing the canalis tentaculiferus of cæcilia (Cope '66 p. 105; '86 p. 442.

X The presence of the rudimentary tentacular apparatus in the larval Amphiuma (Davison '95 pp. 401, 405; '96 pp. 684ff.

XI The "peculiar disposition of the fascial investment" (Davison '95 p. 404.

XII The presence in both of an omo-humero-maxillaris muscle (m. levator maxillæ inferioris ascendens) (Fischer '64 p. 64; Weidersheim '79 p. 66; Davison '95 p. 504.

XIII "The distribution of the cranial nerves in the two species (*sic*) is almost identical" (Davison '95 p. 404.

XIV The existence in both of a ramus lateralis recurrens branch of the facial nerve.

XV The absence in both gymnophiona and Amphiuma of a ductus Botalii.

XVI The derotrematous condition of the young gymnophione paralleling the adult Amphiuma.

XVII The characteristic bipinnate external gills in the young of both Amphiuma and gymnophiona (Hay, Ryder, Sarasins.

XVIII The great length of the trachea and the inequality in the size of the lungs (Davison ,95 p. 404.

XIX The marked metamerism of the mesomphros in both Gymnophiona and Amphiuma (Field '92.

XX The existence in both of a rudimentary type of uninary bladder (Field '94.

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XXI The occurrence, in both, of internal fertilization (Davison '94, p. 48 ; '95 p. 403.

XXII The size of the ova, character of egg strings and the incubatory habits of the parent (Ryder '88 ; Sarasins '90 and '97.

These resemblances, if true, are certainly of importance but it would appear that some of them are of minor value, some are based upon imperfect knowledge or misconception, while some are false. Taking them in order they may be reviewed as follows :—

I Scales, as is well known, exists in the skins of most gymnophiones. Cope ('66) says "it does not appear to have been noticed that [the Amphiumidæ] possess minute scales." In his latest papers (*e. g.* '89) he quotes several times the entire sentence from which the above is taken but each time omitting the three words "possess minute scales," a tacit admission of his mistake. Amphiuma in neither young or adult has scales. The skin, however, contains numerous glands, and these in alcoholic specimens appear like minute white spots and were probably what Cope mistook for scales.

II The abbreviation of the lower jaw in the young is a feature common to all urodeles and is possibly an inheritance from an elasmobranch ancestor. It certainly has little weight as an argument in this connexion.

III That the gymnophiona possess ethmoids has been known since Dugés ('34, pl. xiv, fig. 96, 97.) Study of my sections show it to be, as the Sarasins figures also show it, a true ethmoid (mesethmoid) with the addition of other parts, and that the suggestion of Cope ('95 p. 1110) that it is other than ethmoid is without foundation. According to all authors the ethmoid is lacking from all urodeles and hence Cope's statement that Amphiuma possesses this cranial element was the most important point in his phylogenesis of cæcilians from Amphiuma-like forms. His description "an axial cranial bone . . . . . in front of the orbito-sphenoids" and his unsatisfactory figure throws a possible doubt as to exactly what he refers, but it would appear probable that as Wilder ('91 p. 163) myself ('92) and Davison ('95 p. 403) have suggested his ethmoid was really the perpendicular plates of the premaxillaries and frontals. The detailed description of this region given by Wiedersheim ('77,

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pp. 402 ff) is sufficient to show that the element in question cannot be ethmoidal, for the ethmoidal cartilage remains cartilaginous throughout life.

IV Little weight can be given this point, for no free margin of a frontal can foreshadow the existence of postfrontal and jugal bones, for this is exactly what Cope's statement means. The cæcilian skull is decidely stegocephalic, taking that term in its etymological sense, and this condition has not been derived from any skull like that of urodeles by the addition of bones, but is beyond doubt derived from an ancestral type in which the whole head was covered with membrane bones, among them the postfrontal and the jugals. The skull of Amphiuma is simplified by the loss of bones both in this region and elsewhere; and we can hardly believe that the bones once lost in an Amphiuma-like ancestor can have reappeared in the descendants.

V Of about the same importance is the presence of amphicœle vertebræ, for these are common to perennibranchs, derotremes and many Salamandrina as well as the Stegocephala, and their existence in both Amphiuma and the gymnophiona can, at most, be used only as evidence of descent from an amphicœle ancestor.

VI The vertebral similarities have been discussed by Peter ('94) who, like Cope, is inclined to regard the gymnophiona as aberrant urodeles. In his summary he points out that the chief differences between the vertebræ of urodeles and cæcilians lie in the vental processes, both anterior and posterior, and in the sharp keel on the centra in the latter group. He farther shows that the same processes are very variable in the cæcilians and that similar structures occur not only in Amphiuma but in Siren as well. Later he emphasizes this as follows:—"Um auf Cope's Hypothese zurückzukommen, so ist zwar eine gewisse Aenlichkeit in der Wirbeln bei Apoden [Gymnophionen] und Amphiumiden vorhanden, aber keine grössere als sie zwischen ihnen und Siren besteht, so dass die Ansicht diese Forschers sich hauptsächlich auf entwicklungsgeschichtliche Thatsachen zu stürzen hat. Peters still further weakens (pp. 38-40) the evidence derived from these structures by explaining their similarities as due to homoplassy.

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VII-VIII Cope's reference to Strasser's statement that the cæcilians possess "small cartilages in the position of the inferior elements by (*sic*) the scapular arch" I have been unable to verify. Cope in his bibliography refers to but one paper by Strasser ('79) and in this I find not the slightest allusion to the cæcilians, nor do I find any in his article of '78. However, the existence of rudiments of limbs or girdles can give but little evidence of affinity. Equally little weight can be given to the tendency toward degeneration show by Amphiuma. We know that the limbs were lost in the stegocephalan Aistopoda, which show in their osseous features no approach towards the cæcilians. Hence since limbs have been lost independently in two groups there is nothing improbable in the view that the tendency to loss in Amphiuma, like that in Siren, is without connexion with their loss in the other forms.

IX-X If it be true that Amphiuma has a rudimentary tentacular apparatus or that traces remain of the former presence of such structure, or, lastly, if these be present any feature which seems on the road to development into this organ, elsewhere known only in the gymnophiona, then this one point would go far towards showing close relations between the two groups. A little examination of the soft parts is sufficient to show that the canal cited by Cope as foreshadowing the tentacular canal of the cæcilians is not in the right position for a tentacle and that in reality it is for the passage of the nasalis externus nerve (see Wilder, '92, pl. 13, fig. 6) and hence can be omitted from farther discussion. Davison's description of a tentacular apparatus ('95, '96) is based upon a misinterpretation. Thanks to his kindness I have had an opportunity of examining his slides. I find, and Dr. Davison now agrees with my interpretation, that the so-called tentacular apparatus in Amphiuma was based upon sections cut through a trematode lying in the sub-ocular blood vessel. In this connexion, though not bearing directly upon the matters under discussion, attention might be called to Cope's suggestion ('89 p. 223) that the tentacular apparatus of a cæcilian is homologous with the 'balancer' of a urodele larva. The balancer is apparently a modified external gill, the tentacular apparatus is nothing of the sort.

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XI-XII I have paid no attention to the muscular system and so cannot judge as to the importance of these points.

XIII-XIV The distribution of the cranial nerves agrees in the two groups only in so far as both are amphibians. On the other hand there are marked differences between the two and of such a character that they cannot be explained on the hypothesis of Cope nor on that of the Sarasins, but they are intelligible upon the ground of descent from a common ancestor. This will be referred to later in this paper.

XV A Botal's duct is lacking in Amphiuma (*teste* Boas '81, '82) and in Siphonops (Weidersheim '79) but one is found in Ichthyophis (Sarasins '90).

XVI The derotrematous young gymnophione closely parallels the permanent condition in Amphiuma, but if it prove anything this proves too much, for other forms are also derotrematous, the anura even having a derotreme stage.

XVII That there is a marked similarity between the external gills of the early Amphiuma, Ichthyophis and Hypogeophis (Brauer '99) has been noticed by all who have examined these organs. In both groups there are three pairs of these organs (the third much smaller than the others in Hypogeophis) and at their full development each gill consists of a central rhachis bearing the gill filaments arranged in a bipinnate manner. In the early Amphiuma there is much less regularity and as in my preliminary paper I had only these stages I failed to confirm Hay's description in this respect. Still it must be remembered that Peters ('75) has described the branchiæ of Typhlonectes as broad bladder-like organs. On the other hand the bipinnate type of gill is common in the amphibia, while Clemenz ('94) has shown that, wherever occuring in the vertebrates, external gills are very variable, marked differences occuring even in the limits of the same family. Evidence derived from branchiæ and branchial clefts cannot be decisive and can only have cumulative value.

XVIII From the fact that in ophidia and amphisbænans great elongation of the body is correlated with increase in length of the trachea and inequality in the size of the lungs the similarities between Amphiuma and the cæcilians in the same points can have little weight in settling questions of genetic

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relationships. Besides it must be recollected that great inequality in the size of the lungs of Amphiuma is not constant (*Cf*, Cope '95 p. 1109) but that they may be described as "subequal" while in the gymnophiona there is great inequality, the left lung being almost vestigial.

XIX The metamerism of the mesonephros of the young cæcilians (Ichthyophis) is closely like that of the young Amphiuma and does not occur in anura or in other urodeles. This is, possibly, one of the strongest points in the argument for the close association of the two. Spengel ('76) demonstrated the marked metamerism of the kidney in gymnophiones and his work has been confirmed by the later researches of Semon ('91). In all other amphibia, Amphiuma excepted, this metamerism is at least obscured. Field however has shown ('92) that the metamerism of the mesonephros in the young of this genus is at least as marked as in the cæcilians. Still it is possible that this is really a retention in two lines of what must have been the original vertebrate condition. On the other hand the nephridial structures of the two forms show differences, to be alluded to later which go far towards counterbalancing these resemblances.

XX Field has farther shown ('94) that, using the urinary bladder as a criterion, the amphibia may be divided into four categories according as the urinary bladder is (1) median and elongate, (2) median and saccular, (3) saccular, divided anteriorly into two horns and (4) paired. In the first group are associated Proteus, Siren, Amphiuma and many gymnophiona. But these similarities are of less importance when we recall that where the development of the bladder has been followed in other forms it is found that they pass through the condition occurring in group one before reaching the adult character. Hence the only conclusion that can be drawn is, not that Amphiuma and the gymnophiones are closely related, but that they have remained permanently in a condition which is transitory in other amphibia. In this connexion it may be noted that Cope (*e. g.* '89, p. 36) would deive the amphiumidæ from the amblystomidæ through the Desmognathidæ. But Amblystoma in its development passes through a stage in which the bladder resembles that of the adult Amphiuma.

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XXI It is well known that internal fertilization occurs in gymnophiona and various writers have described the copulatory organs of the males. Davison states ('95, p. 403) that he has demonstrated the occurrence of internal fertilization in Amphiuma as well, and adduces this as additional evidence of the close relationship of the two groups. So far as published ('94, '95) the only basis for the statement is as follows:—He describes in Amphiuma the cloacal folds, so well known in other urodeles, and states that they are not intelligible upon any other supposition than that they act as a series of capillary tubes inducing the spermatozoa within the cloaca of the female. In addition he found in May, a male with ripe spermatozoa and ('94, p. 48) "inasmuch as the eggs are not deposited until August or September, fertilization must occur within the body of the parent." No reason is given for assigning such a late date to oviposition. On the contrary all the published facts would lead one to place the act much earlier in the year. Thus Hay found his eggs, nearly ready to hatch, on September 1st. Ryder ('89) gives no dates for his specimens but merely states that they were recently received and that some hatched in transit from New Orleans. Now since his account was published October 1st this would imply that they reached him in August, or before the middle of September at the latest. The advanced condition of the eggs in both lots (Hay and Ryder) would seem to indicate that they had been laid for weeks, possibly for months, for it is hardly probable that the mother would retain the eggs with their peculiar envelope until they were nearly ready for hatching before depositing them. All this however is neither here nor there. Internal impregnation has not been demonstrated to occur in Amphiuma, and even should later researches show its existence it would be a fact of little taxonomic importance as is shown by the cases of the European species of Salamandra.

XXII The resemblances in the incubatory habits and the size and character of the egg strings in Amphiuma and Ichthyophis have been commented upon by both Ryder ('88) and the Sarasins. In both the female broods over the eggs, but this is a feature shared by various urodeles, for instance; Desmognathus fusca (Wilder '99), Autodax lugubris (Ritter and Miller

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'99), Plethodon cinereus (Montgomery '01). Hence this feature alone has little weight.

The eggs of Amphiuma, about 8mm. in diameter, are nearly spherical and are connected together, like a string of beads by a cord composed of the (in alcohol) hardened common envelope of the eggs. The eggs of Ichthyophis are much the same and in both the connecting cord is spirally twisted. The material of Amphiuma which I have had was in such condition that I could not ascertain whether the details of structure described by the Sarasins in Ichthyophis occurred here as well. If I understand them aright ('87 p. 9) both the cord and its contents are twisted in Ichthyophis and these authors suggest a comparison with the chalazea of the avian egg. Brauer ('97) describes the eggs of Hypogeophis and their envelopes as closely similar to those of Ichthyophis. Yet these similarities between the gymnophione and amphiuman eggs can have little weight when we recall the egg-strings so common in amphibia and realize that all that is necessary to convert the common type into that found in Amphiuma is a diminution of the envelope between the successive eggs. Farther, Hay ('90 p. 13) quotes Whitman as stating that the Japanese Megalobatrachus maximus lays its eggs in a string like that of Amphiuma, and that the eggs are of about the same size.

In conclusion it may be said that from the foregoing it would appear that the only morphological features which will stand as indicating a close affinity between Amphiuma and the gymnophiona are those common to most Amphibia, while the other points such as character of egg-strings, external gills, length of trachea, etc. are of little weight in this connexion, especially in view of the really great differences between the groups in morphological matters which must now be ennumerated.

DIFFERENCES BETWEEN THE CÆCILIANS AND AMPHIUMA AND OTHER URODELES.

The structural differences between the cæcilians and other Amphibia are so great that I think we are fully justified in the recognition of a distinct order gymnophiona. It is true that Professor Cope ('89 p. 443) has objected to Boulenger's ('83)

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characterization of the Cæcilians: "No limbs; tail rudimentary; Males with an intromittent copulatory organ. Adapted for burrowing" on the ground that not one of these characteristics is of ordinal value. They are, however, diagnostic and they are farther supported by a wealth of features which I think prove that, although no fossil gymnophiones are known, the group has long been separated from the other amphibian orders and that the differentiation occurred at a very early period.

Among the skeletal features which may be noted are the following: In the gymnophiona there are ribs upon all the vertebræ except the atlas and a few of the most posterior of these elements. In the longer bodied urodeles, with which comparisons would most likely be made (*e. g.* Amphiuma), the ribs are confined to a few of the most anterior vertebræ (cf. Cuvier '26, Cope '89). In some urodeles like Necturus the conditions are much as in the cæcilians, hence this point, while opposed to close association of Amphiuma and the gymnophiona, is not diagnostic of the former group.

As has been pointed out by various writers from Huxley to Peter ('94) the gymnophiona differ from all urodeles in the absence of a so-called odontoid process,* a feature which is especially well developed in Amphiuma.

The skull is well ossified in the gymnophiona and consists of a greater number of bones than occur in any urodele. It farther differs from all other existing Amphibia in the overarching of the temporal fossæ by the jugal† and post frontal bones. These latter elements are entirely lacking in all urodeles with which I am acquainted. They occur however in the stegocephali. If we regard the urodeles as ancestors of the cæcilians we are at once confronted with the disappearance of these bones in the ancestors and their subsequent reappearance, a difficulty which disappears if we, in accordance with Wiedersheim's earlier views ('79), trace the gymnophiona directly from the stegocephali instead of through the urodeles.

The ossification of the ethmoidal cartilage giving rise to a true ethmoid bone in the gymnophiona was seized upon by Cope ('86) as of great importance from the taxonomic stand-

* This term is used without any attempt to settle its homologies in different groups.

† Squamosal of Huxley, Wiedersheim and Cope.

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point. It is an element entirely lacking from all urodeles,* while in my limited reading upon the stegocephalan skull, I have found not a word concerning its existence or non-existence in that group. Should this region have been cartilaginous in the stegocephali as it is in existing urodeles, then it would appear that ossification in this region had arisen within the gymnophione stock. If, on the other hand, the stegocephals had an ossified ethmoid the remarks made in reference to the jugal and post frontal bones would be equally pertinent here.

A palatopterygoid arch occurs in the gymnophiona, the stegocephali and in some urodeles as well, but some distinctions are to be drawn between the conditions existing in the urodeles and those in the cæcilians. In the former, when the arch is complete, the palatine and pterygoid elements are fused as in Proteus and Necturus, while, when the arch is incomplete, the palatine is usually united with the vomer. In the gymnophiona, on the other hand the palatine is distinct from the pterygoid throughout life, and when it fuses with another element, it unites with the maxillary rather than with the vomer. Farther, as Huxley ('71) has pointed out, the palatines in the gymnophiona "extend back on the inner side of the maxilla in a manner unlike anything observed in other existing Amphibia." Among the stegocephals we meet conditions which can be regarded as ancestral to those found in existing urodeles and cæcilians. Thus in Branchiosaurus we have the palatopterygoid arch incomplete and the palatine approximate to the vomer, while in Acanthostoma and Metopias true palatovomerines occur. In certain genera of labyrinthodonts (Archegosaurus, Cyclotosaurus, Gondwandosaurus and Mastodonsaurus the arch is complete and the palatines extend back along the inner side of the maxilla as in existing cæcilians. Still farther weight must be assigned this palatopterygoid arch, since in just those forms, like Amphiuma, in which the elongation of the body and the degeneration of the limbs seems to point in the cæcilian direction, this arch is most imperfect.

* It is hardly necessary to say that the ectethmoid or sphenethmoid described by some writers (*e. g.* Parker, '77, '79, '81) or the ethmoid of Wilder ('91) is not the element in question.

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The turbinal bone* has less importance. It occurs in but few cæcilians and is lacking in urodeles and, apparently, in the stegocephali, and may possibly have arisen within the cæcilian line. The fusion of basioccipital, parasphenoid, and the otic bones into an os basale is a feature characteristic of the gymnophiona and occurs in no other living batrachia, and apparently not in the stegocephals. Another feature which is shared by cæcilians and stegocephals is the second or vomero-palatine series of teeth which is less perfectly developed in the urodeles.

In the development of the chondrocranium of the gymnophiona Winslow ('98) has shown that these forms differ from other amphibia in the formation of the trabeculæ from two parallel and superimposed rods, in the lack of palato-basal and otic processes to the quadrate (both features pointing to the crossopterygii rather than to the dipnoi), and in the existence of a distinct palatine cartilage.

In the non skeletal parts of the body there are many and important differences between the gymnophiona and the urodeles but since these are in portions not fossilized no comparisons can be made with the stegocephals.

The œsophagus is extremely elongate in the gymnophiona; in the longest of the urodeles it is of moderate length. The intestine is not coiled in the gymnophiona; it is coiled in all urodeles. In the gymnophiona the liver is divided into numerous over-lapping lobes, a condition which does not occur in the urodeles.

In the gymnophiona the heart is carried back to a posterior position in the body unique among amphibia, and this is correlated with some other features. Thus there is an elongation of the truncus and a proportional abbreviation of the conus, while in urodeles the conus is much longer than the truncus. In the cæcilians there is no spiral fold in the conus. One occurs in Amphiuma. According to Wiedersheim ('79, p. 84) cardinal veins are lacking in the gymnophiona; in all urodeles, so far as I know, they occur.

The urogenital system presents many characters of importance and for our knowledge of many of these we are indebted to the

* The nasale laterale of Wiedersheim ('79); the turbinal of the Sarasins ('90). The latter authors have discussed its relations in a satisfactory manner.

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careful work of Spengel ('76), Wiedersheim ('79, Semon ('91) and Field ('92, '94, '94[a]). In the cæcilians the gonads are placed upon the ventral surface of the supporting membrane (mesorchium, mesovarium); in Amphiuma and other amphibia upon its lateral margin. In the gymnophiona the fat bodies are lateral of the gonads; in Amphiuma and other urodeles they are on the medial side of the sexual glands; in the anura anterior to them. The cæcilian conditions have been shown by Semon to be secondary. In the cæcilians the mesonephros is extremely narrow and of about the same width throughout; in Amphiuma it is narrower in front, much broader behind. In the cæcilians the mesonephros presents metameric varicosities throughout life but in Amphiuma this metamerism is transitory (see however p. 328). In the female gymnophiones the Müllerian duct opens in the cœlom near the anterior end of the kidney; in Amphiuma, as in other urodeles and in the anura, the anterior opening is far forward, near the base of the lungs. In the gymnophiona, according to the researches of Semon, the mesonephronic system overlaps the pronephric and hence in some somites both of these systems coexist; in the urodeles there is no such over-lapping, but a gap always exists between the two, the gap in Amphiuma (Field '94[a]) extending over twenty somites. In the young gymnophione (Semon) the pronephros extends through at least twelve somites and the canales principales are metamerically arranged and equal the somites in number. In Amphiuma, on the contrary, the pronephros is in relation with but three somites (Field '94[a]) while in other urodeles but two* somites are concerned in its formation. In the gymnophiona the gonads lie at about the middle third of the mesonephros; in Amphiuma and the urodeles generally, they are in front of the main body of the kidney.

In the cæcilians only one lung is developed, the right one being rudimentary and only a few millimetres in length. In those urodeles which possess lungs there is no such disparity in size and both are functional. In Amphiuma where an inequality occurs the smallest lung nearly reaches the tip of the liver.

* For two exceptional cases (Triton, Amblystoma) see Field '91.

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In the nervous system there are several important features to be noticed which forbid us to regard the cæcilians as closely related to any of the urodeles. Some of these points are summarized below, but there remains much yet to do in this line, especially with regard to the internal structure of the brain.

Superficially the brains of cæcilians (*cf.* Wiedersheim '79, Waldschmidt '87, Burckhardt '91) and that of the young Amphiuma resemble each other rather closely (as has already been pointed out—Kingsley '92) in their longitudinal compression. In each the posterior angles of the cerebrum almost touch the the lateral angles of the medulla oblongata. These resemblances however, are superficial and are brought about by different conditions. In the cæcilians it is caused by the enormous development of the saddle fold in front of the varolian flexure (Burckhardt '91) while in the young Amphiuma the saddle fold is but slightly developed, but the mid-brain region is shortened and the optic lobes are forced between the hinder ends of the cerebral hemispheres.

The cerebral hemispheres are highly developed in the gymnophiona; in most urodeles and in Amphiuma they are not as large as the mid-brain and medulla together. This point, however, has little real value since Burckhardt has shown that the relative proportions of these parts may vary greatly within the limits of the single genus Triton. The olfactory lobes are more strongly developed and more plainly marked off from the cerebrum in the gymnophiona than in the urodeles; this may, however, be correlated with their subterranean habits.

Burckhardt has pointed out the existence of prominences upon the lower surface of the cæcilian cerebrum which he is inclined to interpret as lobi temporales, structures unknown in any urodele. He has also called attention to the appearance, in development, of a cervical flexure in the gymnophiones, a case not paralleled in the urodeles. The roof of the thalamencephalon is arched in gymnophiones, flattened in most, if not all urodeles. The cerebellum also is better developed in the cæcilians than in any urodele.

In the cæcilians (Wiedersheim '89, Burckhardt '91) the olfactory nerve is double from the point of emergence from the brain. No such condition is known to exist in any urodele.

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Wiedersheim formerly laid much stress upon this condition, but Burckhardt has shown that it has another significance from that formerly assigned to it and that it is to be explained by the peculiarities of the development of the ethmoid bone. It has, it seems to me, like the existence of the ethmoid itself, much weight in showing the lack of close relationship between the gymnophiones and the urodeles.

It would also appear that considerable weight is to be given to the relation existing between the palatine branch of the seventh and the various branches of the fifth nerves, which may be briefly stated as follows:—

In the cæcilians (Ichthyophis), as shown by my investigations which remain as yet unpublished, there is an anastomosis between the palatine and the maxillaris superior nerves and no such connexion between the palatine and the ophthalmicus profundus. As these nerves have not been carefully followed in other cæcilians we cannot say what conditions exist in other genera. In every urodele, so far as known, the conditions are exactly reversed, the communication existing between the palatine and the ophthalmicus profundus, and none between the palatine and the maxillaris. This has been shown by Herrick ('94) and Coghill ('01) for Amblystoma; by Miss Bowers ('00) in Spelerpes and by myself ('02) in Amphiuma. I have also satisfied myself that the relations are the same in Desmognathus. According to von Plessin and Rabinowicz ('91) Salamandra maculatus agrees, so far as relations of the fifth and palatine nerves are concerned, with the gymnophiona, rather than with the other urodeles. Somewhat troubled by this I sectioned specimens of the same species and of about the same size (26mm. total length) as those studied by these authors and found them in error (Kingsley '96). The anastomosis between the palatine and the ophthalmicus profundus exists in Salamandra as it does in other urodeles, while that between the palatine and the maxillaris superior is, as in the other urodeles, non-existent. It would appear that these authors, pioneers in a new field and influenced by well known conditions in higher vertebrates, had over-looked the anastomosis which really occurs, and, on the

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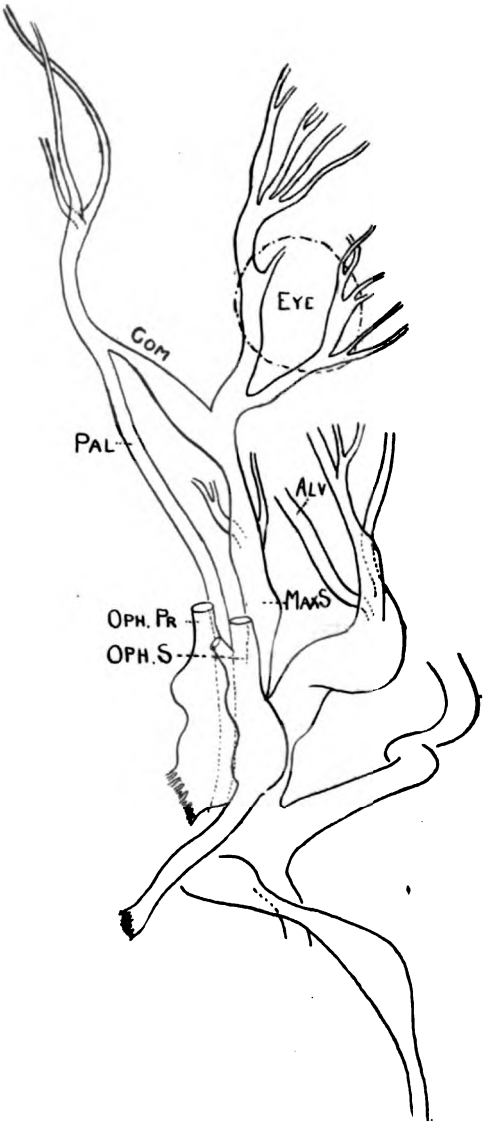
other hand, had interpreted one of the eye-muscles as the connexion between palatine and maxillaris superior.



Reconstruction of parts of Fifth and Seventh nerves of *Ichthyophis glutinosus* *Alv.* alveolaris; *Com.* Commissure between maxillaris superior (*Max. S.*) and palatine (*Pal.*) nerves *Oph. Pr.* ophthalmicus profundus nerve; *Oph. S.* ophthalmicus superficialis.

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Upon the basis of present knowledge, therefore, we may sharply constrast the cæcilians and the urodeles in the matter of relations of the fifth and palatine nerves; and it may be pointed out that here, as in several other features of nervous anatomy, the gymnophiona (*cf.* Burckhardt '91) approach more nearly to the anura than to the urodeles, for, as Arnold has shown ('94) for Pipa, and Strong ('95) for Rana, there exists in both these genera the same anastomosis between the maxillaris superior and the palatine which occurs in Ichthyophis, while in addition Strong describes in Rana an additional connexion farther forward, between palatine and profundus. It is hardly necessary to suggest that these relations, if they be shown to hold good for all members of the groups,—urodeles, anura and gymnophiona,—would indicate a common ancestor in which both commissures existed and that these three groups became distinct before the disappearance of either connexion, closely paralleling the conclusions to be drawn from the cranial structures. It is to be noted that Pinkus ('94) does not describe any ramus communicans between the palatine and the fifth nerve in Protopterus, but that in Polypterus (Pollard '92) there is a connexion between the palatine and the maxillaris superior. So far as this one point has weight it points to a crossopterygian rather than a dipnoan ancestry for the Amphibia.

When, in conclusion, we review the whole series of facts enumerated in the foregoing pages and assign to each what is apparently its proper value, we think we are fully justified in accepting the conclusion of Huxley as true today as when it was written ('78) "none of the Peromela [=gymnophiona] present the slightest indication of an approximation towards the anura or the urodela." In other words the inference that notwithstanding certain superficial resemblances to Amphiuma, the group of gymnophiona cannot be included as a family within the urodeles, nor can Amphiuma be regarded as a neotenic cæcilian but that these interesting forms must be accorded the position of a distinct order of the class of amphibia, and that the only point of union between cæcilians, anura and urodeles must be sought, where Wiedersheim ('79) looked for it, in the extinct group of stegocephali.

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Farther, all evidence of structure as well as the significant fact of discontinuous distribution tends to show that the gymnophiona are an extremely old group, in spite of the fact that fossils of the order are absolutely unknown. It also shows that these same gymnophiona are the most stegocephaline of all existing Amphibia. As such the group deserves far more study than has yet been given it.

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PLATE I.

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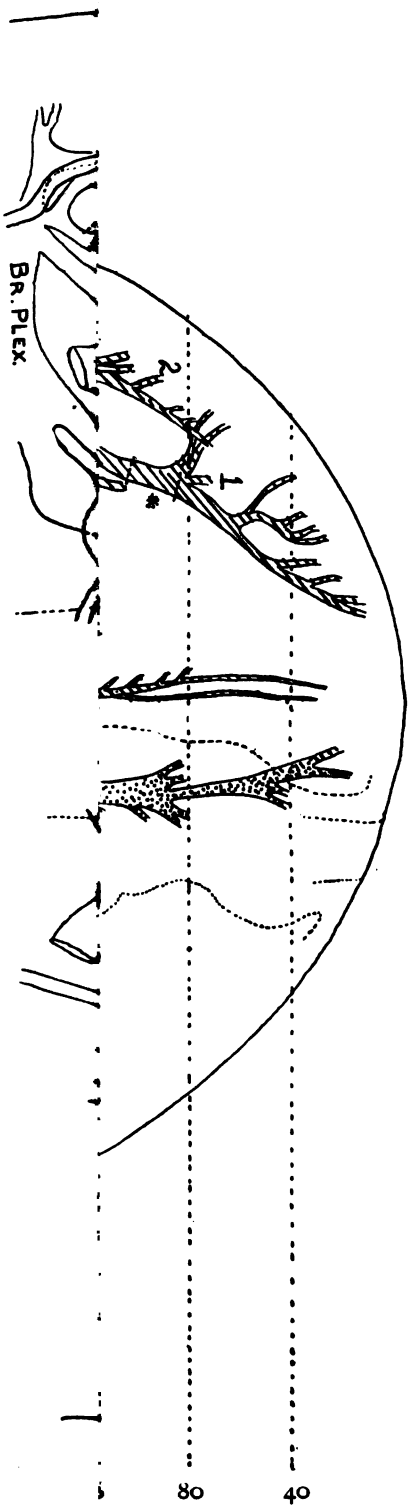

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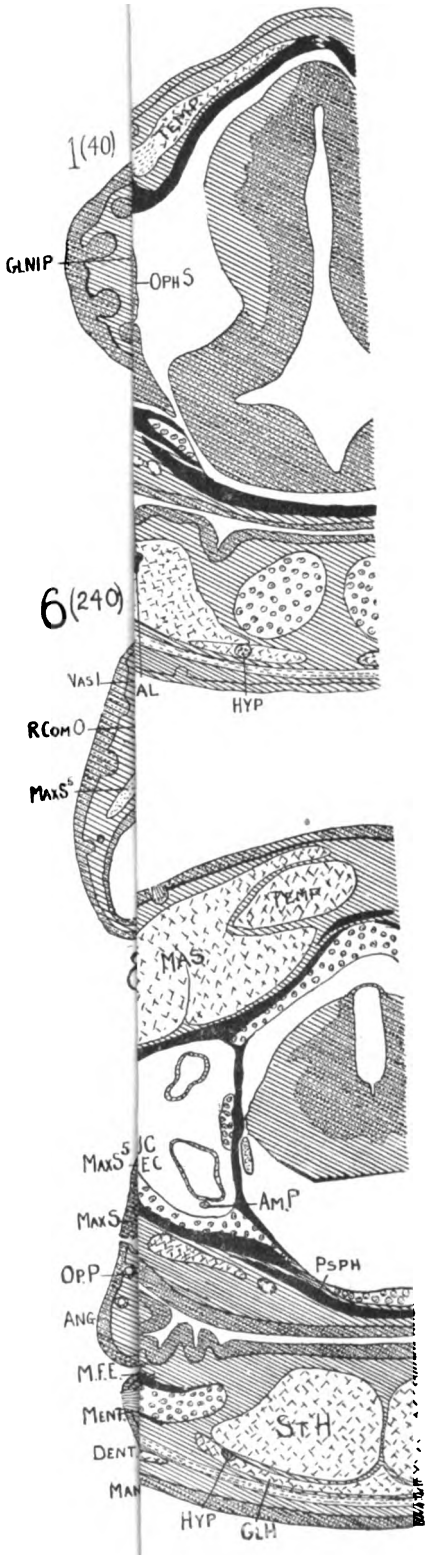

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A DESCRIPTION OF CERIANTHUS BOREALIS VERRILL.

By J. S. Kingsley.

The species of *Cerianthus* inhabiting the coast of northern New England was described by Verrill ('73, p. 5) in the following words:—

"Body much elongated, tapering gradually to the abactinal opening, the surface smooth but more or less sulcated longitudinally. Marginal tentacles very numerous and unequal, in the largest specimens 2.25 inches long and .12 in diameter at base, gradually tapering, acute; the outer ones one inch or less in length. Oral tentacles numerous, crowded in several rows, in the largest specimens about one inch long, slender, acute. Color of body dark chestnut brown, pale bluish just beneath the tentacles; disk pale yellowish brown, space within the oral tentacles, around the mouth, deep brown, with lighter radiating lines; oral tentacles pale chestnut brown, marginal ones dark salmon or light yellowish brown, the longest barred transversely with six or eight dark reddish brown spots, each spot partially divided along the median line into two lateral ones.

"The two specimens, dredged in 28 fathoms, east of Grand Manan, by the writer, measured 5 inches across the disk and tentacles, but their bodies were mutilated. Entire ones of much smaller size were dredged by Dr. Packard and Mr. Cooke in 110 and 150 fathoms, soft mud, near St. George's Bank. The largest of these was 8 inches long, and like other species of this genus, inhabited a thick felt-like muddy tube."

Later ('74, p. 46) Verrill recorded this species from Casco Bay. The same year (Smith and Harger, '74, p. 54) the description is repeated in essentially the same shape with the mention of a specimen from near Seguin Island, Maine, which had a length of 450 mm. and a spread of tentacles of 175 mm. A figure is given (pl. II, fig. 5), and record is made of a small

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specimen from eighteen fathoms, off Watch Hill, R. I. In 1875 (p. 42) Verrill again mentions the last specimen.

With these exceptions no notice has been made of the adult of this species since its first description. What is probably the young was described as early as 1863 by Alexander Agassiz under the name *Arachnactis brachiolata*, from Nahant, Mass.; this account being somewhat extended and illustrated by more figures by Mark ('84, pl. 12; figs. 16-23,) from drawings by Mr. Agassiz. In the plate is shown a young *Edwardsia* which is stated in the explanation to have been raised from a young *Arachnactis*. This introduces an element of doubt. In *Arachnactis*, as in all stages of *Cerianthus*, there is, as has often been pointed out, an odd number of tentacles, while this *Edwardsia* is described as having sixteen. Another fact would seem to indicate that some confusion has occurred, since in *Cerianthus* there are two circles of tentacles, oral and marginal, and the latter begin to develop at an early date in the *Arachnactis* stage. In *Edwardsia*, on the other hand, only marginal tentacles are present. A skilled observer like Mr. Agassiz would be more apt to confuse embryos than to overlook a second series of tentacles or to make a mistake in his count of the number of marginals, when the total did not exceed sixteen or seventeen. Another matter must be taken into consideration. Mr. Agassiz's early work was done at Nahant, and since *Cerianthus borealis* is an inhabitant of the Gulf of Maine, its *Arachnactis* larva might be expected to occur at Nahant. On the other hand the larva from which his *Edwardsia* was raised came from Newport, R. I., and *Cerianthus* is at least rare in New England waters south of Cape Cod. According to the strict laws of priority (which are frequently more honored in the breach than in the observance) were it definitely shown that *Arachnactis brachiolata* was the young of *Cerianthus borealis* there are those who would maintain that the specific name *brachiolata* should hold.

There is a second matter of nomenclature. In Koren and Danielssen's "Fauna Litoralis Norvegiæ" ('77, pl. iv, fig. 8) is an illustration of a *Cerianthus* in its tube, but neither in text nor in the explanation of the plates is there any reference to it. Eleven years later this specimen was described by Danielssen

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('88) as *Cerianthus borealis*. He copies this figure, with others illustrating anatomical details and states that it was not described in the earlier work, because it was then believed to be identical with *C. lloydii* of Gosse. Later, the reception of authentic specimens of that species convinced him that the Norwegian specimens were distinct, hence it was described as a new species. The name *borealis* however cannot hold here for it was preoccupied fifteen years before by Verrill, as we have seen, for the perfectly distinct species which is the subject of the present paper. For the Norwegian species of Danielssen the name *Cerianthus danielsseni* may be employed.*

Before beginning the account of *Cerianthus borealis* it is necessary to consider how the various terms 'dorsal' and 'ventral,' 'anterior' and 'posterior,' 'sulcus' and 'sulculus,' etc. are to be applied.

Kölliker, studying the Pennatulids, spoke of that side of these animals which bear the longer gastral filaments as 'dorsal' while those directives which had the shortest filaments were termed 'ventral.' From this as a basis these terms have been transferred to other Anthozoa, but without uniformity in their use. Since in the stomodæum of these Alcyonids there is but a single siphonoglyph, and this is 'ventral' in position, it has been assumed by some that in other Anthozoans where there is but a single siphonoglyph (*Peachia*, *Cerianthus*, some Hexactinians) this must be homologous with the ventral siphonoglyph of the Alcyonids, and this orientation has pervaded much of the recent literature.†

*Faurot ('95, p. 221) in a paragraph which includes a number of errors (including the statement that Danielssen described *Cerianthus borealis* in 1876, and by implication, that McMurrich is the authority for *C. americanus*) is inclined to think that the various forms known as *lloydii*, *borealis* (Danielssen) and *americanus* are but members of one species, the well-known *C. membranaceus*. While it is possible that some of the European forms—*vogti*, *danielsseni*, *abyssorum*—may be synonymous with older known species, the American *borealis* and *americanus* are certainly distinct.

† It is to be noted, however, that Van Beneden ('91) has objected to this terminology, and, influenced by homologies supposed to exist between the Cœlenterates on the one hand and Annelids, etc. on the other, has proposed to replace the terms 'dorsal' and 'ventral' by 'posterior' and 'anterior' respectively. So, too, Haddon ('89) believing that these terms 'dorsal' and 'ventral' are misleading has called the two syphonoglyphs sulcus (ventral) and sulculus (dorsal) these terms being, to his mind, preferable to the 'gonidium' and 'gonidulum' of Andres ('84) on account of the ease with which other terms—sulcular, sulcar, etc.—may be made from them. These, however, are matters of terminology and do not affect the main question.

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Haacke ('79) however, claims that these comparisons are not conclusive, and, that, in fact an element of error has been introduced. He regards the single siphonoglyph of *Cerianthus* as dorsal. Carlgren ('93) attacks the same problem and is lead to agree in results with Haacke. The outline of his argument is as follows:—In the Alcyonaria (Octocoralla) the longitudinal septal muscles are on the sides of the septa which are turned *towards* the single siphonoglyph, hence these muscles are to be regarded as turned ventrally. In *Cerianthus*, according to Carlgren, all of the septal muscles are turned *away from* the siphonoglyph; hence the siphonoglyphs are not homologous in the two groups. Since the terms 'dorsal' and 'ventral' were first introduced in the Octocoralla, their meaning there must be adopted in other Cœlenterates and consequently the siphonoglyph of *Cerianthus* must be dorsal. In this he is followed by Bourne ('00) among others, who states that the ciliated groove of *Cerianthus* "is the sulculus, the sulcus being absent."

When *Peachia*, *Zoantharia* and other forms are taken into account the problem becomes more complicated. In these genera the three pairs of longitudinal septal muscles are turned towards the single siphonoglyph (sulcus, Haddon*), while the pair on the ventral directives are turned towards the opposite pole. Hence there is not here the certainty that there seems to be at first glance in the comparison between *Cerianthus* and the Alcyonaria.

The order of formation of the septa affords another test of the matter. In the majority of Hexactinians and *Edwardsiæ*

*Haddon says ('89 p. 300) "In adult Actiniæ with two œsophageal grooves it is not possible to distinguish which is the sulcar and which the sulcular groove; nor when only one groove is present can we in all cases determine which it is. Probably it will be found that, in every case where one groove only is present during the whole life it is the sulcar groove. But in the case of the genus *Sagartia* (Gosse; *s.s*) [and as Parker has shown, in *Metridium*] one groove is as often present as two. There is no reason, as far as is known, to regard this as the sulcus. It appears more probable that the one grooved condition is a secondary feature, and the groove may be either the sulcus or the sulculus."

The later observations of Torrey, ('98) Parker, ('99) and Mrs. Davenport ('03) upon *Metridium* and upon this same genus *Sagartia* would seem to confirm the opinion of the last sentence for they make it probable the monoglyphic condition is the result of longitudinal fission. and hence the siphonoglyph would be sulcar in one and sulcular in the other of two individuals resulting from the division of a single diglyphic individual.

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where there is evidence upon the point, there is a regular sequence, there being at one stage four pairs (not couples) of septa present. These arise, passing from one end to the other in the order 3, 1, 2, 4, and only later do septa 5 and 6 arise which transform the primitive plan of 8 into the adult hexacorallan condition. Of these eight, the pairs 4, 2 and 1 have the septal muscles pointing in one direction while those on 3 face the other way. So far as I am aware the order of formation of the septa in *Peachia* and *Halcampa* has not been traced from the first, but according to Haddon's figures ('87, pl. xi, especially fig. 7) it would appear probable that the order was the same as in the diglyphic species. These genera, however have but a single siphonoglyph, which lies at the end of the body where (apparently) the third pair of septa (directives) must occur.

It is the concurrent testimony of all who have studied the ordor of the development of the septa in *Cerianthus*—H. V. Wilson ('88), Boveri ('89), Van Beneden ('91), and McMurrich ('91)—that the first four pairs arise in the sequence which is followed in the normal Hexactinians, and that the pair of directives at the siphonoglyphal end are the third septa in the order of appearance and hence the siphonoglyph of *Cerianthus* is homologous with that of *Halcampa*.

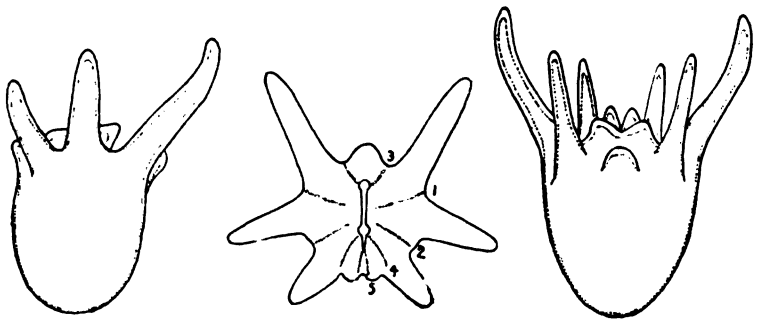

FIG. 1.—Side, oral and sulcar views of Arachnactis from Casco Bay. 1, 2, 3, 4, 5 Septa in order of appearance.

But this does not settle the matter so far as the Alcyonarians are concerned, nor can we, with our present knowledge, use the same method with that group, for, so far as I am aware, the

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four pair of septa in the Alcyonaria are formed simultaneously (Korschelt and Heider, '95 p. 78). So the problem presents two alternatives when the attempt is made to homologise *Cerianthus* with that group. Is greater weight to be laid upon the position of the siphonoglyph or upon that of the muscle banners? With my limited knowledge of Cœlenterate morphology I am not competent to decide, yet a specimen of *Arachnactis* (fig. 1) collected in Casco Bay possesses some interest in this connection. In this specimen nine tentacles and five pairs of septa were present, thus making the embryo a little older than Van Beneden's last stage. In this specimen length of septa and development of mesenterial filaments tend to support the views of previous writers as to the order of formation of the septa.

It may, however, be pointed out that tentacles 3 are longer than the others. The mouth is especially noticeable. In Van Beneden's figures ('91, pl. I fig. 9; pl. IV, fig. 1) there is a siphonoglyph at either end of the mouth. In the Casco Bay specimen development has gone farther. At one end is a well developed siphonoglyph embraced by septa 3, while near the other end, just beyond septa 4 is a groove on either side of the œsophagus, *i.e.*, just in the position of the second siphonoglyph in Van Beneden's figure. But the mouth has extended beyond this point by interstitial growth in the middle of the earlier siphonoglyph. These facts show that the ancestral form was diglyphic.

I have not been able to confirm, in my specimens, Carlgren's discovery of the longitudinal septal muscles in *Cerianthus*, but do not deny their presence. As he shows them in his diagrammatic sketch ('93, p. 245, fig. 2^3) they are represented as throughout on the face of the septa turned from the directives, although he nowhere explicitly states this to be the case with the fourth pair. "So weit ich habe finden können tragen diese Cereantheen auf der von dem Richtungsseptenpaar abgewandten Seite longitudinale, auf der entgegengesetzten, gegen die Richtungssepten zugewandten, transversale Muskeln." If the figure be accurate it follows that in *Cerianthus* either one or more probably three pairs of septa have become inverted, as compared with the typical hexacorallan. If, then, the muscles may de-

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velop on either side of the septa and if originally *Cerianthus* had two pairs of siphonoglyphs, we are left without a basis of comparison with the octocorallans. In view of all these facts I think it best to restrict the terms sulcus and sulculus to those forms where the order of septal formation can be followed, the sulcus, following Haddon, to be the groove occuring in Halcampa, *i.e.* that at the end marked by septa 3, the sulculus being at the opposite end between septa 4. According to this view *Cerianthus* possesses throughout life a sulcus, the sulculus, which appears in the early *Arachnactis* is soon lost. The terms

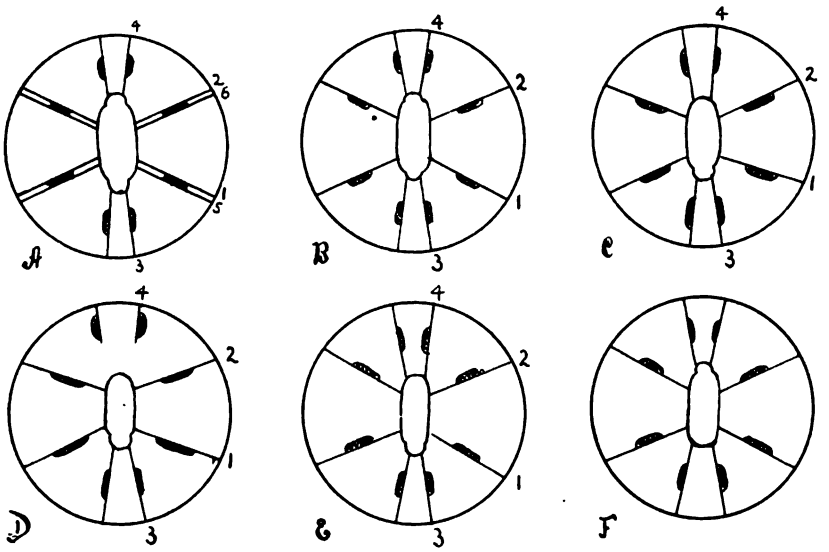

FIG. 2.—Diagram of the relation of septa, sulcus, and sulculus in, A, normal Hexactinian; B, *Edwardsia*; C, *Halcampa*; D, *Zoanthus*; E, *Cerianthus*; F, Alcyonarian.

'dorsal' and 'ventral' may be retained for the Alcyonaria, for any transfer of sulcus and sulculus to that group, or of 'dorsal' and 'ventral' to the Hexacorallans implies homologies which at present cannot be proved to exist.

As Verrill's descriptions do not touch upon anatomical details and since other students do not appear to have seen his

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Cerianthus borealis the following account of specimens in the Barnum Museum of Tufts College is given here. The preservation of these is not the best and hence all points cannot be described as fully as could be desired. The specimens are five in number, all coming from near Casco Bay, Maine. One was obtained on a trawl line by Dr. F. D. Lambert in the summer of 1901 at a depth of 70 fathoms on 'Great Ledge' near Seguin Island. This is the best preserved of any. The others were taken by Captain John Toothaker, of South Harpswell, Maine, on trawls during the winter of 1902-03 and were presented by him to the College. These five specimens will be referred to in the following account as A, B, C, D, and E. Two or three of the Arachnactis larvae have been taken in the tow at the South Harpswell Laboratory.

The animal lives, like its congeners, in thick felt-like tubes of mud and fine sand agglutinated by mucus secreted by the numerous mucus glands in the body wall and by entangled nematcysts. Many if not all of these tubes ('sheaths' of the fishermen) contain Sabellid worms (? *Myxicola*) as commensals.

EXTERNAL CHARACTERS

The body is somewhat fusiform, being largest at a point a little above the middle and tapering slightly to a region just beneath the tentacles, but more rapidly towards the aboral end, which is abruptly rounded, with the terminal pore characteristic of the genus. The surface of the body is nearly smooth, being marked with numerous faint longitudinal impressed lines; which, as sections show, do not correspond in position to the septa.

At the base of the tentacles the body expands in a vase-like manner, the column ending with the circle of marginal tentacles. These are closely crowded in several rows, those of the outer series being shorter than the inner. It was not an easy matter to study the relations of these to the septa nor to the tentacles of the inner series nor to ascertain whether Fischer (*'89*) or Faurot ('95) was correct in the interpretation of their arrangement in *C. membranaceus*. These authors worked with specimens in which the tentacles were less than seventy in number in either

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series, but with this number doubled, as it is in all the specimens I have had, the difficulties are greatly increased and I have not been certain in my results. It is to be noted that Fischer has corrected Heider in this matter and has been corrected in turn by Faurot.

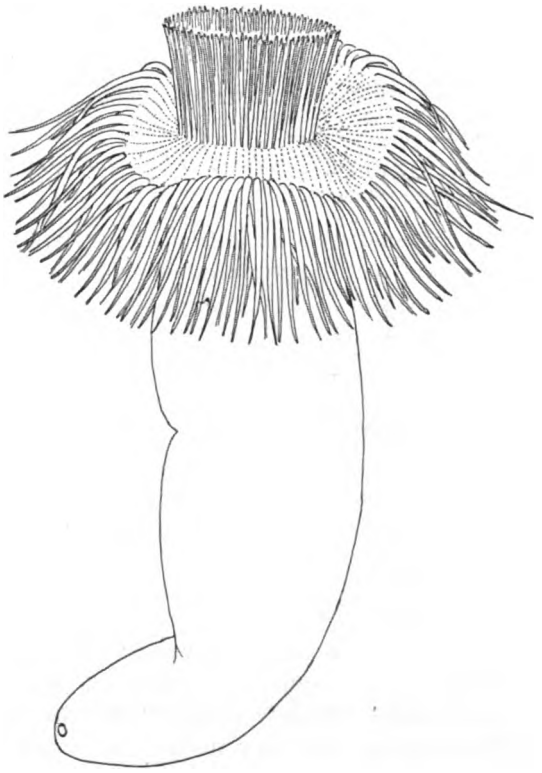

FIG. 3.—*Cerianthus borealis* Verrill.

The marginal tentacles are slightly contracted at the base, expand a little distance above their insertion and then taper gradually towards the tip, the terminal portion being somewhat filamentary in character.

The disc, between marginal and oral or labial tentacles, is more or less funnel-shaped, the labial tentacles being placed at a lower level than the others. The outer portion of this disc is

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strongly grooved, the grooves corresponding in position to the septa. The labial tentacles are nearly equal in size and are more slender and more uniform in their tapering than the marginal ones.

The following statistics show that our specimens do not vary greatly among themselves. All measurements are in millimeters.

	A	B	C	D	E
Length from base of tentacles to aboral pole	128	190	142	144	205
Length of longest marginal tentacle		62			
Expanse of tentacles and disc		130	115	120	160
Largest diameter of column	40	50	38	37	41
Number of marginal tentacles	139	155	141	159	157

Specimen *A* differed somewhat from the others in color. It was a dark chestnut with lighter reddish tentacles, now faded in alcohol to a dirty yellow. The others were a dark slate gray, about the color of the mud in which they live, and our specimens show no such change of color at the base of the tentacles as is described by Verrill. The outer marginal tentacles are, on the outside and near the tips, about the color of the column; the inner surface, like the other tentacles of both series being a shade of red best described as a very dark salmon. After being in alcohol for a few days none showed any traces of the banding described by Verrill.

INTERNAL FEATURES

The wide mouth (a wide, nearly circular opening in the alcoholic specimens) begins immediately inside of the labial tentacles. The œsophagus depends from it into the interior. In specimen *A* this was thrown into transverse folds and was 21 mm. in length; in *B* it showed no contraction and was 33 mm. long. Its inner surface is finely marked with longitudinal impressed lines, corresponding to folds in the high columnar ectoderm and not to the insertion of the septa on its outer surface. At opposite ends are two grooves, the siphonoglyphs. One of these, the sulcus, is of considerable breadth. Its surface is much smoother than the rest of the œsophagus and is about five or six millimeters across. The other groove which has a similar appearance is much smaller, hardly a millimeter in width,

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From the account of the structure in *Arachnactis* as given above it will be seen that this can be compared only to the median part of the sulculus of the earlier stages. It is small and has been over-looked by several writers. Indeed it would seem to vary in size, as would naturally follow from the method of growth in this region. Thus Heider ('79) says that in many specimens of *C. membranaceus* "könnte ich kaum mehr eine Andeutung derselben finden." Haime ('54) speaks of it as "qu'un sillon droit, étroit, et faiblement accusé," while his figures show merely a depression with few of the features of a siphonoglyph. Vogt ('88,) Danielssen ('88) and McMurrich ('90) neither figure or describe a groove in this region, while Faurot ('95) mentions it as the 'petit sillon.'

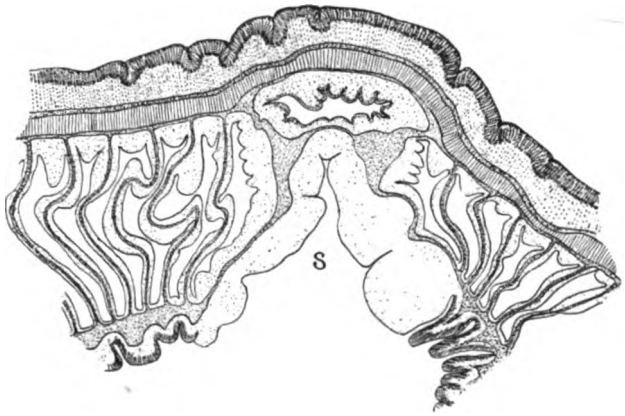

FIG. 4.—Section through sulcus, *s*, body wall, and a few of the septa.

Cerianthus borealis differs from some of its congeners (*C. membranaceus*, *C. americanus*) and agrees with others (*C. lloydii*, *C. danielsseni*) in the great extension of its septa. In *C. membranaceus* (*teste auctorum*, *inter alia* Faurot, '95) only two septa reach to the aboral pole, the others falling far short. In *C. americanus* (according to McMurrich '90 p. 137 pl. II fig. 1.) ten septa reach the aboral pole, the others being much shorter. In *C. danielsseni*, according to Danielssen ('88) there are but eight pairs of septa, and of these, all except the directives, judging

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from his figures, reach the aboral pole. In *C. lloydii* (Carlgren '*93a*) about 21 reach "in allgemein" to the aboral pole. No statements are made by Danielssen ('*90*) for *C. abyssorum*, but in *C. vogti* he speaks of three or four septa on each side of the 'continuing septa' (i.e. septa 1) that reach to within a few millimeters of the aboral opening.

The arrangement of the mesenteries in *C. borealis* agrees most closely with the description given by Fauret of those in *C. membranaceus*. I was not able with my material to settle all points but the following account is approximately correct. Five

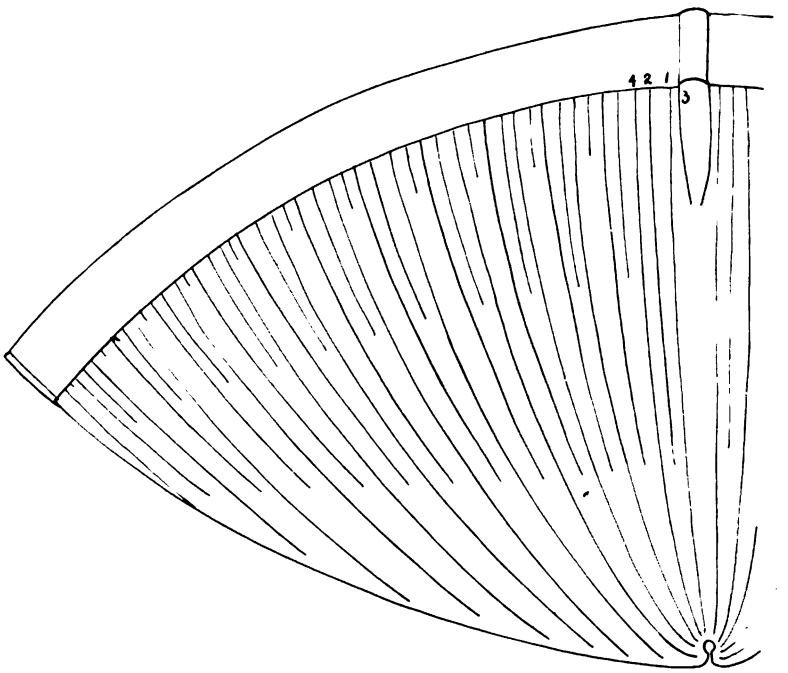

FIG. 5.—Diagram of arrangement of septa in Cerianthus, opened along the sulcular line; a little over half the animal shown. 1, 2, 3, 4, the first four septa formed; the relative lengths of primary, secondary, tertiary and quaternary septa is shown.

pairs of septa on the sulcar side reach to within a millimeter or two of the aboral opening, there being a slight difference be-

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tween them in length. Between the most sulcar in position of these longer septa (i.e., between the homologues of the 'continuous septa' of *C. membranaceus*) are a pair of much shorter septa, the sulcar directives (septa 3) which are hardly a fifth part of the length of the body. The septa next beyond the continuous septa (septa 2) reach about three-fourths of the body length while the next pair, fourth in order from the sulcus reach almost to the aboral pole. These four septa on either side are apparently the septa 3 (directives) 1, 2 and 4 of the Arachnactis stage. Beyond this point and passing towards the sulcular side the arrangement is like that described by Faurot or better as illustrated by Delage et Hérouard ('01, p. 672) for *C. membranaceus*. There is the same arrangement in 'quatroseptes', which, however, can be better expressed by grouping the septa in four categories—primary, secondary, tertiary and quarternary—according to length, the primary being the longest. These alternate, proceeding from the sulcar to the sulcular side, in the order 1, 3, 2, 4. 1, 3, 2, 4, etc., one of these repetitions forming a 'quatrosepte' of Faurot.

Five pairs of the primary septa (including 1 and 4 of the Arachnactis stage reach, as was said above, to within a short distance of the aboral opening, but from this point the successive primaries become shorter and shorter, the ends of the two of a pair (right and left) being opposite each other on either side of the sulcular plane. The secondary septa do not reach as far, while the tertiary are much shorter, and the quarternary scarcely extend below the œsophagus on the sulcular side. All of the primary and secondary septa bear gonads on their aboral halves, but only a few of the longest septa of the tertiary series have these organs and no reproductive bodies are found on the septa of the quarternary order (Fig. 6).

The result of the order of length (and of order of appearance) of the primary septa is to produce an arrangement on the sulcular side which is strongly suggestive of the arrangement of the sclerosepta on the principal septal side of a Tetracorallan.

The material upon which I have worked was not prepared for histological study and hence has not afforded good sections. I have, however, been able to make out that, like *C. membrana-*

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ceus, *C. vas* and *C. lloydii* and unlike *C. danielsseni*, *C. vogti*, *C. americanus*, *C. borealis* is hermaphroditic. Ova and testicular follicles are intermingled in each septum without any regularity; and in the testicular follicles there is the same radial arrangement of the spermatozoa noticed and figured by Heider in *C. membranaceus*. The eggs, somewhat contracted by the preservative fluid are more or less granular from the enclosed yolk particles, which are more abundant in the larger eggs. The oval nuclei are markedly excentric in position and do not stain at all (with Delafield's hæmatoxylon) with the exception of a large deeply-staining nucleolus in each (Fig. 7).

SUMMARY

(1) The name *Cerianthus borealis* has been applied to two species, by Verrill in 1873 and by Danielssen in 1888. Danielssen's species from the Norwegian coast may be called *C. danielsseni*.

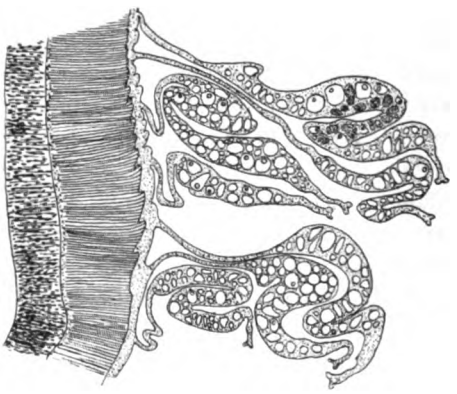

FIG. 6.—Section through body wall and septa showing gonads in septa of primary, secondary and tertiary orders.

(2) The terms sulcus and sulculus were the first applied by Haddon to the siphonoglyphal grooves in *Halcampa* and allied forms. The larger and more prominent siphonoglyph in *Cerianthus* is homologous with the single groove in *Halcampa* and

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hence should be called sulcus, and not sulculus as is maintained by Bourne.

(3) Contrary to the views of Haacke, Carlgren et al., it is not possible at present to decide whether the single siphonoglyph of the Alcyonarians is homologous with the sulcus or with the sulculus of other forms; hence the retention of the terms dorsal and ventral in that group is warranted on the grounds of their non-committal character.

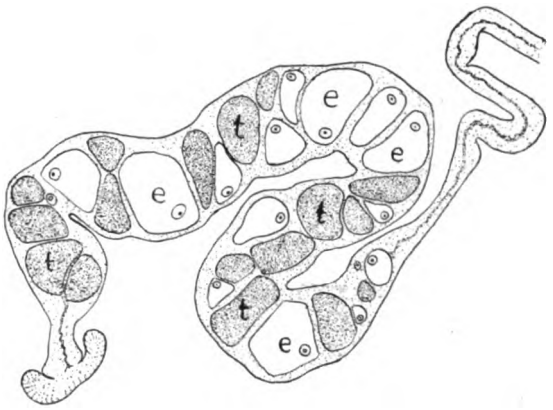

FIG. 7.—A single septum showing the eggs, *e*, and the testicular follicles, t.

(4) *Cerianthus borealis* is distinguished from *C. danielsseni*, *C. vogtii* and *C. americanus* by being hermaphroditic. It differs from *C. membranaceus* and *C. lloydii* in the great extension of its septa, five pairs reaching to the aboral pole; and from *C. vas* McMurrich ('*93*) in the presence of tentacles (?) and the greater number of mesenteries.

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THE HYPOPHYSIS IN AMBLYSTOMA

By J. S. Kingsley and F. W. Thyng.

I. Historical and Critical.

The older history of our knowledge of the development of the hypophysis in vertebrates has been well summarized by Minot ('92 p. 575) whose account, with a few alterations is given here.

The older authors regarded the hypophysis as a part of the brain; this conception was held by von Baer (in his Entwicklungsgeschichte, i, p. 104*, 1828, and ii, p.293, 1837), and found a defender in F. Schmidt (Zeits. wiss. Zool., xi, 1862) although Rathke (Müller's Archiv, 1838, pp. 482-485) had discovered the [ectodermal] hypophysial invagination, his discovery being confirmed by Kölliker (Entwicklungsgeschichte, 1861, p. 242) yet Rathke later (Entwicklungsgeschichte, 1861, p. 200) withdrew his opinion that the evagination formed the hypophysis,† but W. Müller ('71) showed that the hypophysis unquestionably arose from the evagination, and maintained that the invaginated tissue arises from the entoderm ('Schlundepithels'). That the evagination belongs to the oral cavity [*i.e.* is ectodermal] was finally proven for Amphibia by A. Götte (Unke, 1875) and for mammals by Mihalovics (Entwicklungsgeschichte des Gehirns, Leipzig, 1877.)

The ideas of Götte and Mihalovics, confirmed as they apparently were by numerous observations on various groups prevailed undisputed for several years. Indeed Balfour, in his Comparative Embryology, gives no suggestion of other than an ectodermal origin for the hypophysis, and O. Hertwig, in the third edition of his Lehrbuch (1890) refers to the idea of entodermal contributions to this organ as an exploded one.

* The text reads "An der Spitze des Trichters bemerkt man ein kleines Knöpfchen, den Hirnanhang der noch wenig vom Trichter getrennt ist, und vielleicht einer Verwachsung der Spitze des Trichters seinen Ursprung verdankt." We find no reference to the hypophysis on p. 293 or adjacent pages of the second part.

† He states that he has seen the ingrowth in snakes, birds and mammals, but says that every part of it disappears and that the hypophysis is developed from parts in front of the unpaired trabecula.

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Still later than these summaries are the works of His, Gaupp, Aby, and Lundborg. His ('92) incidentally includes figures of these parts in the frog, axolotl and salamander, in which only ectodermal parts are recognisable, and the same is true of Gaupp's account ('93) of the development of the hypophysis in *Anguis fragilis* and *Lacerta agilis*. Gaupp figures a large Seessels pocket but this is not mentioned in the text as contributing to the organ. In Aby's photographs of sections illustrating the development of the hypophysis in the cat ('93) only ectodermal contributions are recognisable, and Lundborg ('94) finds the structure wholly ectodermal in *Salmo*, axolotl and *Triton*.

In 1894 von Kupffer returned to the idea that the hypophysis was formed by an ingrowth of ectoderm, together with contributions from the infundibulum, but stated that the entoderm also participated in its formation. His work was done on *Rana fusca*, and he figures, in larvae of 3.5 and 4.5 mm. body length two ingrowths, one from the ectoderm above the oral plate, and the other behind it from the roof of the entodermal part of the digestive tract. These two lie in close association with each other and are regarded as forming the anterior and posterior parts of the definitive organ. He also studied other vertebrates and came to the conclusion that the double condition was characteristic of all. He also maintained—his palæostoma theory—that the ectodermal hypophysial ingrowth together with the entodermal part represent the ancestral mouth, a view advanced in part by him a year earlier ('93).

Since 1894 the views upon the origin of the hypophysis have been as divergent as they were before the work of Götte and Mihalovics, some maintaining that both germ layers, ectoderm and entoderm, contributed to it, some that it is purely ectodermal, and a few that it is exclusively entodermal.

Thus Valenti, in a series of papers ('94, '95[a], '95[b], 95[c], '98) claims to confirm the observations of von Kupffer in *Bufo*, *Bombinator* and the chick, while Nusbaum ('96) thinks that he finds a double origin in the dog. Gaupp (1897, pp. 93 and 94; 1901, pp. 8-10) quotes von Kupffer's account and copies two of his

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figures. Gregory ('02) also finds a double origin in the saibling (*Salmo alsaticus*).

On the other hand Pollard ('94) in *Gobius capito*, Haller ('96) in a long series of vertebrates, Dean ('96) in Amia, Salzer ('97) in the pig and guinea pig, Minot ('98, who merely says he has confirmed and extended the results of Haller,) Corning ('99) on two species of *Rana*, and Zeleny ('01) in three species of turtles recognise only ectodermal constituents. This view is accepted in the recent text-books of Gegenbaur ('98, pp. 777-779 and O. Hertwig ('00, pp. 269-272), these authors not even mentioning the possibility of entodermal participation.

A third view is advanced by Prather ('00) who claims that in *Amia* the hypophysis is derived from the entoderm alone.

When these accounts are analysed and the figures studied it is seen that in many instances the evidence presented is not conclusive. Thus von Kupffer's figures are too schematic and show cell outlines with a distinctness which does not occur in early amphibian material; Pollard's work was done exclusively on transverse sections, the most unfavorable for settling the the matter, especially if it be as obscure in the teleosts as would appear from Gregory's paper. Valenti's accounts are very brief and his stages inadequate to settle the matter. He merely describes outgrowths from both ectoderm and entoderm in the early stages and jumps to the conclusion—certainly not warranted by anything shown in his figures—that they unite to form the hypophysis. Dean gives no details regarding *Amia* and merely expresses an opinion. Haller deals largely with the adult condition and has studied only a few early stages; and the same is true of Salzer who apparently only studied the development after the oral plate had broken through. He also describes (p. 58) a part which separates from the hypophysis and later reunites with it, a condition which might possibly be brought into harmony with Nusbaum's work which is ignored by Salzer. The material which Corning studied was not well preserved and the shrinking as shown by his figures was sufficient to tear apart any entodermal-hypophysial connexions which may have existed, and, so far as his plates can decide, the evidence is insufficient for either view. In many of the figures

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of Gregory the limits between what he calls ectoderm and what entoderm are not very evident although in some (*e.g.* figs. 29, 31, and 32,) two points of proliferation are clearly shown. In this summary the only attempt has been to point out the insufficiency of the evidence and the impossibility of basing any certain conclusions upon it. The remaining papers by Zeleny, Nusbaum and Prather are not open to such criticisms as shown by their figures; but they adopt three different views. Mr. Mast informs me that he has studied the development in *Amia* and finds that Prather did not see the early stages of hypophysis formation in that genus, and that it actually has an ectodermal origin.

With this diversity of interpretation we have studied the development in *Amblystoma* where we have had abundant material, the results of which are presented here.

II. Development in Amblystoma.

The earliest stage found which shows any trace of the differentiations which are to produce the hypophysial structures were embryos of about 4 mm. total length, in which the neural

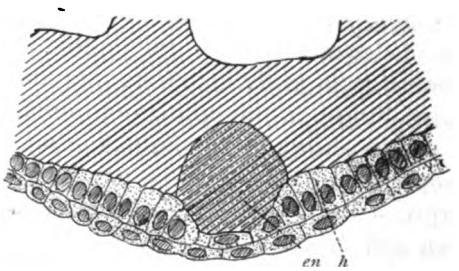

FIG. 1.—Tranverse section of embryo of 4 mm. length showing at *h* the paired origin of the hypophysis.

Reference letters used in all cuts:—*a*, archenteric cavity; *ce*, cuticular layer of ectoderm; *ec*, ectoderm; *en*, entoderm; h, hypophysis; *hs* hypophysial stalk; *i*, infundibulum; *ms* mesenchyme; *n*, notochord; *ne*, nervous layer of ectoderm; *oc*, optic chiasma; *oe*, oral (ectodermal) epithelium; *op*, oral plate; *p*, pinealis; *t*, tooth germ.

folds have met and the anterior neuropore has completely closed, and in which ectoderm and entoderm have fused to form the oral plate. In a transverse section (fig. 1) passing just in front

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of the oral plate, the sensory layer of the two layered ectoderm shows a slight thickening on either side of the median line, in which the cells are decidedly columnar in character, passing over into a more flattened condition to the right and left, while

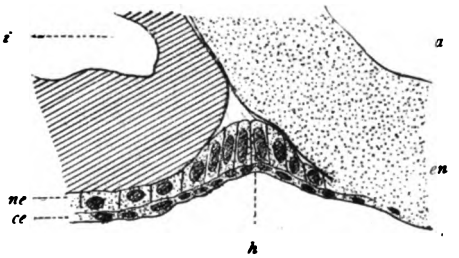

FIG. 2.—Longitudinal section of same stage showing the early thickening of the ectoderm (*ne*) to form the hypophysis.

the cuticular layer shows no modification in passing from side to side. In parasagittal sections of the same stage, passing through the same region (fig. 2) the same columnar condition of the cells is shown.

In embryos slightly older (4.5 mm. long) these thickenings, as shown in transverse sections (fig. 3) have become much more

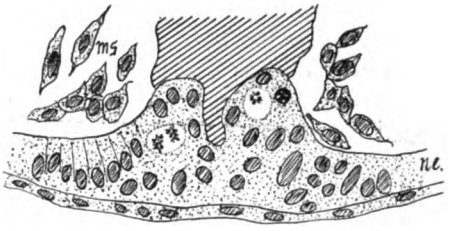

FIG. 3.—Transverse section of an embryo a little later than fig. 1. The paired hypophysial thickenings still remain and mitotic figures show that rapid proliferation is taking place.

marked, the increase being due to active cell proliferation, numerous mitotic nuclei being found in this region. Even now the paired ingrowths exhibit a tendency towards fusion in

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the middle line, which in a little later stage (fig. 4) becomes complete. It is thus seen (as has been known to one of us for many years) that in *Amblystoma* the ectodermal hypophysial anlage is paired in its early stages. A similar paired origin has

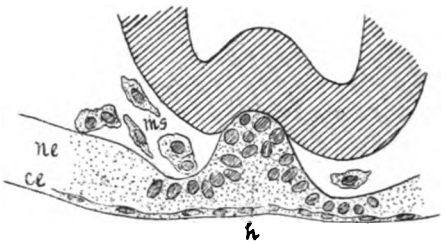

FIG. 4.—A still later stage. The hypophysial ingrowths of the former figure have fused into a single one.

been described by Dohrn ('81), by Gaupp ('93) in saurians, by Pollard ('94) in *Gobius*, by Lundborg ('94) in *Salmo*, and by Gregory ('02) in *Salmo* and *Esox*.

From this early condition this ectodermal anlage gradually extends itself upwards and backwards* until its apex lies immediately adjacent to the infundibulum, and between it and the anterior superior wall of the archenteron (fig. 5). At this stage the apical portion retains the solid many-celled condition it had in the earlier stage, and sections cut in various planes show no regularity in the arrangement of the nuclei. This distal portion is still connected with the parent layer of undifferentiated ectoderm by a flattened stalk in which can readily be recognised two layers, closely applied to each other, as if they formed the walls of a collapsed tube. The two walls are perfectly distinct and show marked differences from each other, although these may not be of morphological significance. The anterior wall, which abuts against the brain, is composed of cubical or columnar cells, while those of the posterior wall are flattened. It will be noticed that the outer or cuticular layer of the ectoderm passes backwards from the hypophysial stalk across the oral plate as a continuous, uninterrupted sheet.

*For purposes of description it is immaterial whether this be regarded as an actual ingrowth or whether the apex remains fixed and the parental ectodermal layer changes its position—See Orr, ('88).

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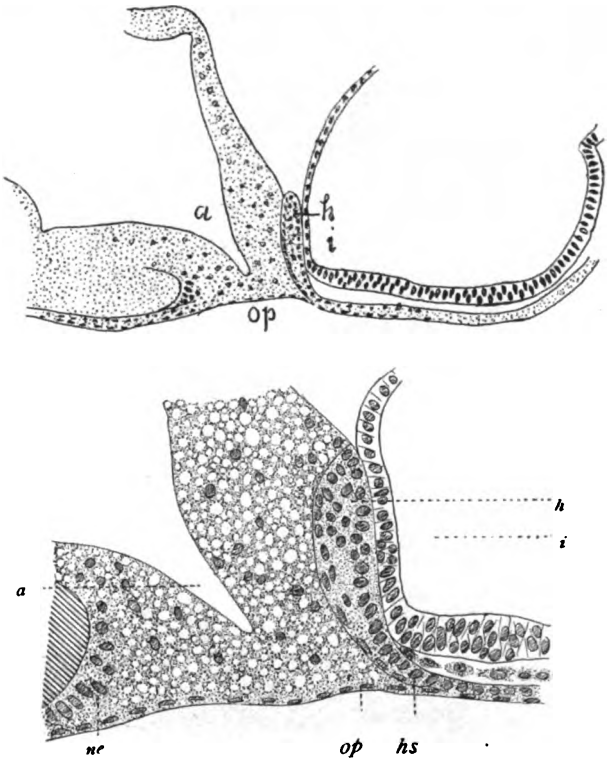
Another point, of some importance later, is to be seen at the posterior (left) margin of the oral plate. There, as will be readily seen (fig. 5) the cells of the nervous layer leave the rest of the ectoderm and bend upwards around the anterior end of of the mass of mesoderm, their nuclei becoming distally indistinguishable from those of the undoubted entoderm. In other



FIGS. 5 and 5A.—Longitudinal sections through an embryo showing the archenteric cavity (*a*) near to the surface of the oral plate. (*op*); the hypophysial stalk (*hs*) and the inward migration of the nuclei of the nervous layer of the epithelium (*ne*) at the posterior border of the future mouth.

words, there is, both in front and behind the oral plate, an ingrowth of the ectoderm, and this posterior portion eventually forms the floor of the anterior part of the mouth. The same conditions can be seen in transverse sections as is shown by

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fig. 6, representing a slightly later stage. Here the sensory layer of the ectoderm on either side of the oral plate curves inward around the ventral ends of the myotomes, and may be traced as a marginal row around the sides of the solid entoderm and dorsally to it to the neighborhood of the hypophysis. In other words these two sections show that the oral plate is a thickened mass of both ectoderm and entoderm, the ectoderm extending further inward the older the larva. Another point which

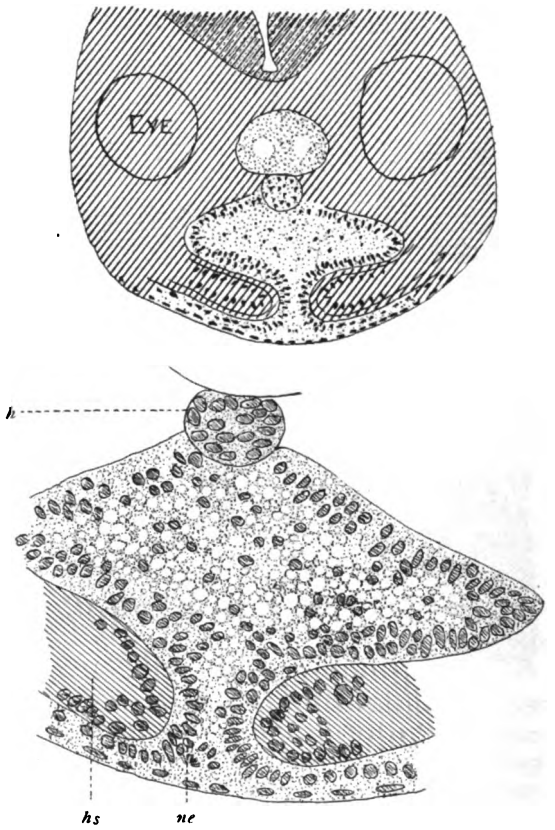

FIG. 6.—Transverse section showing the manner in which the nervous layer of the ectoderm (*ne*) passes inwards around the yolk-bearing entoderm and upwards to the roof. In sections a little in front of this, these marginal nuclei are seen to be continuous with those of the hypophysis (*h*).

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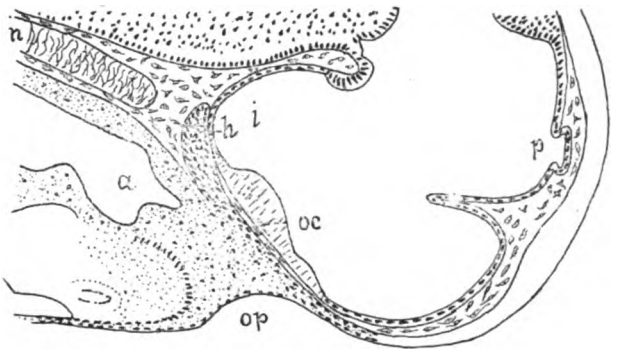
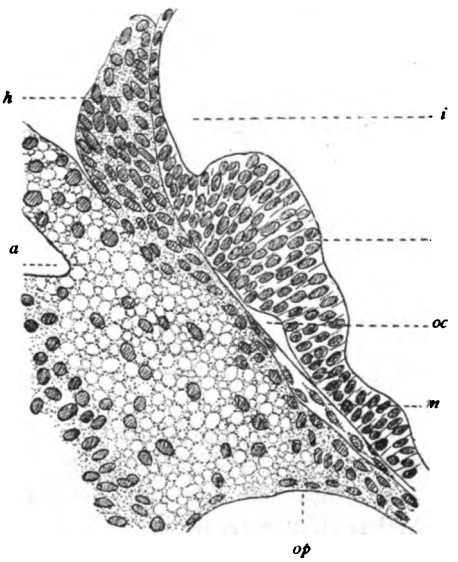
needs mention is the forward extension of the anterior part of the archenteric cavity in the earlier stages as in figs 5 and 5A *x* and its greater distance from the exterior in the later stages as shown by fig. 7A.





FIGS. 7 and 7A.—Longitudinal sections of a later embryo, showing the archenteron (*a*) further removed from the surface than before; the breaking down of the boundary between the hypophysial stalk and the yolk bearing cells of the oral plate and the closely packed immigrant nuclei at the posterior wall of the future mouth.

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In the next stage (fig. 7, sagittal, fig. 8, transverse) the oral plate has greatly thickened and (7A) the ectodermal nuclei at the posterior surface are still seen extending inwards to form the floor of the mouth. On the dorsal surface the distinction between the cells of the hypophysial stalk and those of the oral plate are less evident than earlier, but still there is a more or less plain arrangement of the nuclei in two layers leading to the hypophysis proper, which has now considerably increased in size and which is separated distally from the entoderm by a considerable space into which the mesenchyme is insinuating itself. As will be seen the anterior part of the archenteric cavity (*a*) is now about on a level with the lower end of the hypophysis proper, but is separated by a larger interval than before from the outer surface of the oral plate. In the cross section (fig. 8) it

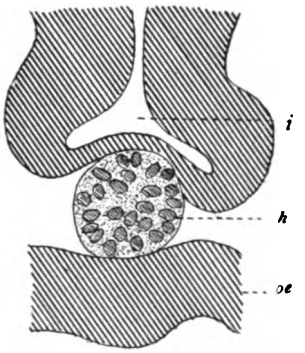

FIG. 8.—Section of the hypophysis at about the stage of fig. 7, showing the encroachment of the hypophysis (*h*) upon the infundibular cavity.

is seen that the distal part of the hypophysis makes a marked indentation in the surface of the infundibulum. (As the section passes obliquely through the infundibular wall, this wall is represented as thicker than it really is.)

In a still later stage, about equal to Clarke's ('79) fig. 16, the mouth is still closed (fig. 9) its anterior part being filled with a mass of irregularly arranged nuclei imbedded in scattered yolk granules, while further back the cells are more or less clearly arranged in two layers. In this specimen some shrinkage had

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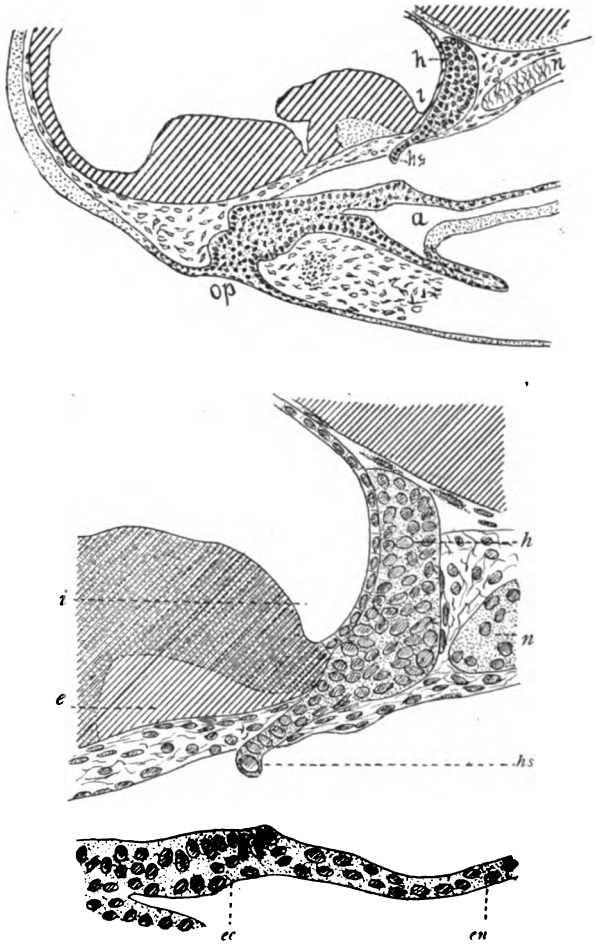
taken place so that the roof of the oral cavity had separated from the structures lying above. In this roof is seen a projection with closely packed nuclei, while directly above it is the



FIGS. 9 and 9A —Longitudinal section shortly before the opening of the mouth. By contraction in preservation the oral epithelium has separated from the super-adjacent tissues, pulling out the hypophysial stalk (*hs*). As will be seen, the nervous layer of the ectoderm continues above and below as an unbroken sheet around the yolk laden cells of the oral plate while behind the point where the hypophysial stalk was attached to the parent layer, the tissue changes to the entoderm (*en*) which is but a single cell in thickness.

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end of the hypophysis pulled out from the surrounding mesenchyme by the separation of the layers, (see also fig. 10) indicating an intimate connexion between the oral roof and the hypophysis. At first we regarded this as a clear indication of an entodermal contribution, but sections of stages intermediate between this and that of fig. 7 show that the connexion is in reality the same as in that stage; that is, this part of the roof of the oral cavity is ectodermal. A little behind this (see fig. 9A) the epithelium of the roof becomes but a single cell in thickness and this probably indicates the line of junction of ectoderm and entoderm.

That this view is correct is shown by transverse sections of about the same stage (fig. 10) which cut through the anterior

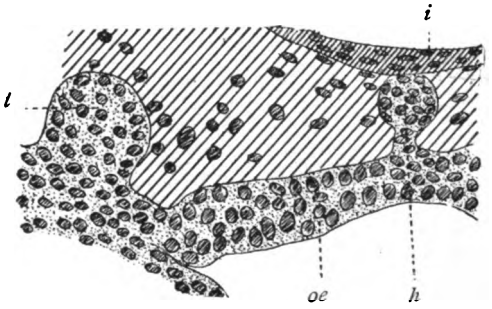

FIG. 10.—Transverse section through one side of oral cavity at about the stage of fig. 9. The hypophysial stalk (*h*) still retains its connexion with the parent layer of the definitive epithelium (*oe*) of the mouth. The mouth itself is not open but the cells of its roof pass over into those which form the tooth germ (*t*) arising from the lateral part of the oral plate.

part of the oral cavity in the middle, and at the sides through the solid mass of both oral layers. Just lateral to the fusion of roof and floor is seen a tooth germ, showing conclusively that the ectoderm extends inward to at least that point. In the middle line is also seen the connexion of the stalk of the hypophysis with the oral roof.

This matter is explained by the way in which the mouth becomes broken through. There is evidently the formation of a stomodæum here, but its cavity becomes filled with yolk cells

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and hence does not present the typical appearance seen in *Petromyzon*, for example. This ingrowth pushes back the entoderm (*cf.* figs. 5 and 7) and then the yolk cells included between the stomodæal walls are gradually absorbed, the absorption, of course, taking place at the posterior end and continuing forward (*cf.* fig. 9) until at last all is absorbed and the lips are free.

The connexion of the hypophysis with the roof of the mouth continues for some time after the mouth is open and the animal begins to feed (figs. 11), but we did not ascertain the exact stage in which the continuity is broken nor have we traced the later history of the organ.

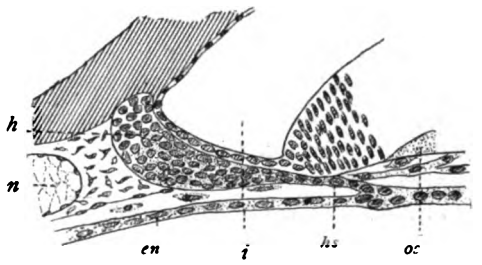

FIG. 11.—Longitudinal section after the breaking through of the mouth, showing the persistence of the hypophysial stalk (*hs*) and the single cell layer (*en*) of the entoderm behind the point of the hypophysis.

III. CONCLUSIONS.

There is nothing in the history of the hypophysis as we have traced it which supports the 'palæostoma theory' of von Kupffer. Its origin as a paired structure would negative this, for it could hardly be supposed that the vertebrates could have had two distinct mouths developed from two successive pairs of gill slits; nor does it present gill-slit features, for it comes into intimate relations, not with entodermal structures but rather with the infundibulum. The paired condition and the columnar cells recognised in the early stages would imply that it was originally either a glandular structure or that it was sensory in character. The later history—so far as it has been traced here—does not suffice to decide between these two possible functions.

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It long remains in connexion with the outside world by a structure, the hypophysial stalk, which in the amniotes is distinctly tubular in character and in *Amblystoma* clearly shows traces of such a condition (*e.g.* fig. 5.) Such a tubular connexion may be interpreted as either a duct for the paired gland or as a tube to convey water to the sense organ at its extremity, the tube lengthening to accommodate the removal of the organ from the exterior caused by the cephalic flexure.

In spite of the disrepute into which the annelid theory of the origin of the vertebrates has fallen in the minds of some, it still has more evidence in its favor than has any alternative as yet proposed, and we have as yet seen no serious objections advanced toward the view that the infundibulum represents the annelid stomodæum. We do not accept the conario-hypophysial mouth of Owen but are inclined rather to favor the speculations of Cunningham ('85) which show that in every respect, except a breaking through into the entoderm, the infundibulum may be compared with the fore gut of the annelids. If this be so it is difficult to explain the relations of the hypophysis as either sensory or glandular. From its connexion with the exterior it could not act as a sensory organ to test matters passing the mouth, nor if it were a gland could its secretions, emptied as they must have been at some distance from the mouth, have had any influence upon digestion, while on neither glandular nor sensory hypothesis is it easy to explain the close relation of the organ with the infundibulum.

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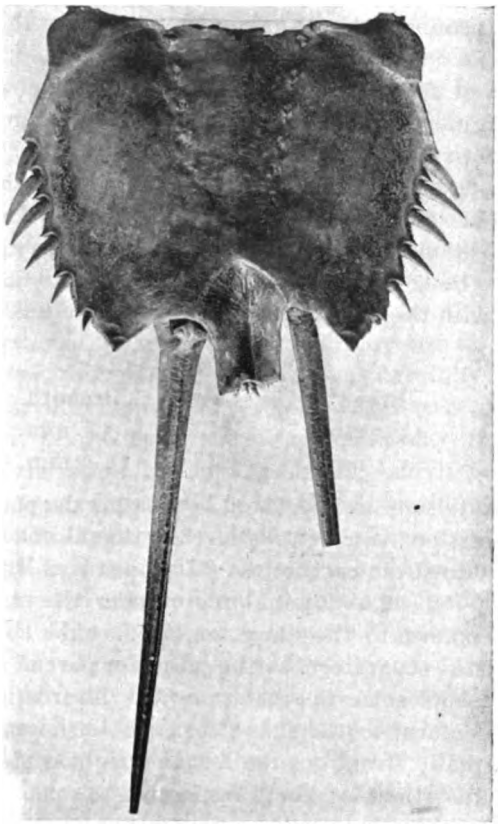
NOTES ON A BICAUDATE SPECIMEN OF *LIMULUS POLYPHEMUS*

By Frederic F. Smith

Duplicity of the longitudinal axis has been so rarely recorded for any arthropod that interest may be taken in a case which has recently come within my observation.



Bicaudate Limulus.

The animal in which this abnormality occurred was a fairly large sized specimen of *Limulus polyphemus*. It was taken at

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Orleans, Massachusetts. Unfortunately the finder did not appreciate the desirability and practicability of preserving his capture in a fluid medium, but allowed it to dry, and threw away the cephalothorax with its appendages, the gill books, and the abdominal viscera. The dorsal shield of the abdomen with its regular and a supernumerary telson or caudal spine is thus the only part saved.

The extreme breadth of the abdominal shield immediately in front of the first pair of lateral spines is 157 mm. Aside from differences connected with the extra telson, the abdomen appears normal. In one minor particular there seemed to be a slight indication of a greater development of the left side, that bearing the regular and larger telson. This difference was in connection with the lateral spines: those of the left side were slightly longer and stouter in the few cases where uninjured spines on both sides allowed fair comparison. Perfect comparison could be made only in two of the pairs, so this evidence is scarcely to be considered, though if admitted it is interesting as agreeing with the greater development of the telson of that side.

Left	Lateral spines		Right	
Length	Breadth	Pair	Breadth	Length
23.5 mm.	5.4 mm.	II	5. mm.	22.5 mm.
17.3 mm.	5.1 mm.	IV	4.9 mm.	16.2 mm.

The two telsons are separated by a rather deep and sharply defined depression; the centres of their dorsal condyles are about 44mm. distant from each other. It appears as if there had been a tendency for the abdominal region near the insertion of each telson to conform to the shape which it would have had if that telson existed separately, so the posterior part of the abdominal shield presents some approach toward bifurcation. The tendency to conform to the shape for each telson taken separately was not equally strong for the left and right abdominal regions near the insertions of their respective telsons, and this is in accordance with the fact that in every respect the left or regular telson is more developed than the right or supernumerary one. From this greater tendency of the left side to conform to the regular form for its telson, the intermediate depressed area be-

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tween the two telsons is associated in greater part with the left telson, and its two movable spines are to the left of the sharp dividing line between the two sections of the intermediate area. These apparently are developed as 'images' of spines on the lateral margin. Lack of room prevented more than two so developing, and these are small and crowded together, close to the line of division already mentioned. No such spines occur on the right portion of the depressed area, but as this is only about two-thirds as wide as the other section, absence on this side is not surprising.

Both telsons show they have been broken off sharply some distance back from where the tips presumably were in an uninjured condition. I am told this was done by careless handling after the animal was taken. However, only about one-fourth is probably missing from the left, and about one-half from the right telson. The left telson seems to have been normally developed in all respects, and at its insertion is the anus. This telson has regularly formed condyles or articulations, has sharply defined edges, and is slightly larger than the other in area of cross-section. No anus could be discovered at the base of the right telson, though the specimen was carefully softened by soaking for several hours. This telson had only an imperfect development of the condyles for articulation. It seemed significant that the outer half of the dorsal condyle was much like the normal type, apparently as on the outer side there was less to interfere with regular development. The ventral tuberosities were small, apparently as the space left was much narrower than that for the corresponding features of the left telson. The edges of the right telson were somewhat less sharply defined than were the edges of the other, and its triangular cross-section was less perfect. The serrations on the edges were less marked than normally. The range of flexion for the two telsons was quite different, as determined upon the softened specimen. The left had a horizontal range of 87°, a vertical range of 108°; the corresponding figures for the right were 40° and 53°. Evidently these differences were accounted for in part by the wide, rather shallow space left for the left telson, and the narrower, deeper space left on the right side. The right telson was in-

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serted more deeply in the opening left for it, and this interfered still further with its range of motion.

Interesting questions occur as to what extent this abnormality corresponds with the few recorded cases among arthropods which appear to be at all similar. Bateson, in his *Materials for the Study of Variation*, makes a distinction between division of median structures and duplicity of the median axis, but shows that this distinction cannot always be recognized. In the present instance duplicity of the axis would certainly seem to be involved, though not to so great an extent as in the two cases of two-tailed scorpions referred to by Bateson (p. 565) as nos. 879, 880. In these there is doubling of a considerable proportion of the whole number of abdominal segments. In some repects this case suggests Bateson's no. 712, (p. 457,) a third instance among the scorpions. Here "the terminal poison-spine was double, ... the two halves were not quite equal and there was no opening of a poison gland on the shorter spine."

I gratefully record my indebtedness to Mr. Solon Higgins of Orleans, Mass., who kindly presented me the specimen.

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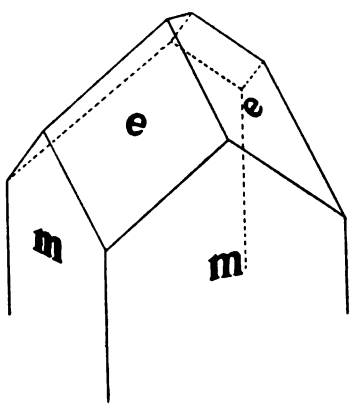
A NEW HABIT FOR CHALCOPYRITE.

RALPH W. RICHARDS.

A specimen of chalcopyrite, collected in Somerville, Massachusetts, by Prof. A. E. Dolbear, of Tufts College, some years ago, shows apparently a new and simple habit for the species. The specimen was found in a vein of rusty quartz in the quarry between Broadway and Holland Streets near Clarendon Hill. The rock of the quarry is the so-called Cambridge or Somerville slate, referred by some geologists to the Carboniferous, by others to the Lower Cambrian. This rock is a clay-slate cut by many diabase dikes which in turn are cut by numerous veins carrying a great variety of minerals, among which quartz, calcite, albite, prehnite, babingtonite, erythrite, chlorite and oxides of titanium recently discovered by Prof. Charles Palache, of Harvard University, may be mentioned.



The crystallization of chalcopyrite is tetragonal and a sphenoidal habit usually predominates. Prof. S. L. Penfield, in his paper in the American Journal of Science on crystals from Chester Co. Pa., (vol. xl, 1890, pp. 207-211) figures specimens showing prismatic and pyramidal planes and others showing sphenoid

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and scalenohedral faces, which he suggests may represent a prism and a second order pyramid distorted by oscillatory combination with the positive sphenoid. The indices he assumes for the distorted forms agree with the forms found on the crystal described in this note.

The Somerville specimen is shown in the cut and possesses only two forms, a prism *m* and a second-order pyramid *e*. These have the indices 110 and 101 respectively and present the identical faces figured by Prof. Penfield, in a twin crystal (Amer. Jour. Sc. *l. c.*, Fig. 8, p. 210). The rough character of the Somerville crystal permitted only contact measurements and the best readings were selected by choice. The angles giving the most satisfactory set of readings are those around the coign *m* to *e*, *e* to *e*, and *e* to *m*. These angles are nearly equal and were found by measurement to be about 60°. This satisfies the relation that should obtain between the plane of the prism and those of the second order pyramid,

e to *e*, 59° 30.5′
e to *m*, 63° 46.1′

In Hintze's Handbuch der Mineralogie, sixteen cases are noted of the occurence of the form *e*, and only seven of *m*. With the exception of one or two cases either one or the other or both forms are subordinate. The Somerville crystal seems novel in showing these forms predominant and perhaps, excepting the sphenoid, represents the simplest form of the crystallized mineral.

It is interesting to note that this form differs very slightly from the isometric dodecahedron. This similarity is accounted for by the axial ratio of the mineral, 1 : .98525. The resemblance of the crystal to the dodecahedron is well brought out by comparing it with a model of the same. In the drawing and in the crystal itself the illusion is destroyed by the downward extension of the prism plane.

The crystal is unusually large for the species having an average diameter of four centimetres. The largest of the Chester County crystals had diameters of a centimetre. Lacroix mentions large crystals from Oued Allelah of Algerian Africa having diameters of eight millimetres. The rather indistinct sphe-

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noids from Ellenville, N. Y. have about the same dimensions as the Somerville crystal.

Credit is due to Prof. Palache, for assistance in the examination of the specimen and suggestions in regard to its importance.

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THREE CASES OF ABNORMALITY IN URODELES.

By Guy M. Winslow.

Within recent years a new interest has arisen in the study of those extreme cases of variation which are commonly called 'abnormalities.' Perhaps no one has contributed more to this interest than Bateson, particularly in his "Materials for the Study of Variation." In this work and in other more recent papers the fact is emphasized that there is an order even in abnormalities and that it is by a study of these extreme cases that we are most likely to gain a better knowledge of all variations, normal as well as abnormal. It is hoped that the following paper may add a little to the accumulating material bearing upon this most interesting and important problem.

Case I. Amblystoma punctatum with bifid toe.

This specimen is an adult Amblystoma with the fourth toe of its right hind foot bifid. The nature and extent of the deformity are shown in figs. 1 and 2. It is entirely confined to the region of the third and fourth joints.

In place of the usual single articular surface at the distal end of the third joint, we have here an enlargement and division of this end of the bone, with two articular surfaces lying in planes inclined at angles of about forty-five degrees to that of the corresponding normal surface. The fourth joint (fig. 2) is represented by two distinct bones each of which is apparently normal in everything but position. The symmetry about the median axis of the toe is almost perfect.

Case 2. Plethodon glutinosus with bifid tail.

This also is an adult animal, the general appearance of which is shown in fig. 3. Its length, measuring from the nose to the end of the longer, left, branch of the tail was seventy millimeters. The right branch was about three millimeters shorter than the left, and, when in the usual position, was inclined at a greater angle from the general axis of the body. Owing to imperfect

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technique the series of sections made of the region where the branching of the tail occurs does not allow a careful study of the finer points of anatomy. A few grosser points of some interest are, however, to be seen. These are represented in figs. 4 to 8.

In fig. 4, the most anterior section of the series, we have the vertebra still single but greatly broadened. The notochord is here fully two and one half times its width in the more anterior normal vertebræ. The muscles (*lm*) are all included in two clearly seperated lateral masses, and their fibres are all cut transversely. In the succeeding figures, 5 to 8, the process of division is gradually carried further, complete separation of the branches taking place a few sections posterior to that shown in fig. 8.

As shown in the drawings, which represent the sections as viewed from the front, the left branch is a little larger than the right in this region, but aside from this the two lateral halves of the sections are approximately symmetrical as are also the corresponding sections of the two branches after their complete separation. A distortion of the vertebræ (figs. 6-8) gives them the appearance of having developed under the influence of a stress which pulled their dorsal and ventral parts toward the median line and away from the more firmly fixed branches of the notochord; and the presence of two bundles of transverse muscle fibres (figs. 5-8 *tm* and *tm'*) make it apparent that this stress was due to their contractions. The anterior of these transverse muscles is quite small (fig. 5 *tm*), but the posterior is of considerable size, and, as we approach the point of division its position upon the vertebræ is gradually taken by the longitudinal muscles (figs. 6-8, *tm'* and *lm*).

It seems probable that this is a case of 'superregeneration.' As is well known, the tail of Plethodon is very easily detached. A study of the tissues of this tail gives evidence which, though not unquestionable, leads me to believe that it is relatively younger than the more anterior parts of the body. The experiments of Tornier ('97) and others in producing similar abnormalities by cutting off the tails of salamanders give added probability to this view.

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CASE 3. A FIVE-LEGGED AMBLYSTOMA PUNCTATUM.

Among a lot of one year old Amblystomæ collected in Middlesex Fells, Mass., the writer found one having a fifth leg. The abnormality was not discovered until after this specimen, together with the others, had been killed and fixed in Kleinenberg's picro-sulphuric acid. It was sectioned in paraffin and the sections were stained in Delafield's hæmatoxylin and eosin. The cartilages, muscles, the abnormal portion of the intestine and the adjacent portions of the lateral muscle and normal intestine were modelled in wax, while the diagrams of the nerves and blood vessels were made by the aid of the common method of reconstruction from camera drawings of the sections.

The total length of the specimen was twenty-seven millimeters, and its stage of development and the position of the abnormal leg are shown in figure 9. This leg projected forward and outward from the side of the body a little in front of and below the proximal end of the normal right leg. As seen before sectioning it appeared to be a fairly accurate mirror image of the normal leg, slightly displaced in a ventral direction. Although by no means perfect in detail this may be considered as a fair example of this class of symmetry.

The skeleton of this leg (figs. 10 and 11) is composed of a pelvic girdle, femur, tibia and fibula, a tarsus of ten cartilages, and ten cartilages belonging to the phalanges.

The girdle has the general features of the normal girdle, from which, however, it differs considerably in detail. It is smaller than the normal girdle, (see fig. 22,) and, like the rest of the leg, reversed in position, so that its pubic portion is but a short distance in front of and below the pubic portion of the normal girdle (fig. 22 *pu'*). The pubic cartilage is perforated by a small obturator foramen (*of'*). The ilium (*il'*) is considerably shorter than the normal ilium (*il*) both absolutely and relatively. This fact, added to the slightly more ventral position of the abnormal girdle, places a considerable distance between the dorsal end of its ilium and the nearest point of the vertebral column. The ventral position of the abnormal girdle is apparently due to the action of gravity in the absence both of any opposing and

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counter-balancing structure on the other side of the body, and of a sufficiently strong support on its own side.

According to the theory of centripetal inflence , (Wiedersheim '93, p. 153) the presence of the abnormal ilium in the region of the thirteenth and fourteenth vertebræ might have been expected to excite growth in the transverse process of one or both of these vertebræ and in the more distal connective tissue, thus producing a corresponding sacrum and sacral rib. It may be owing to the relatively great distance which separates the abnormal ilium from the vertebræ that no such result has occurred.

It is interesting to note, however, that there is a slight symmetrical enlargement of the transverse processes of the seventeenth vertebra (fig. 22, *17*), but with no sacral rib to bring this vertebra into connection with the ilium as occasionally happens.

The femur is of about the normal length, but it is considerably thicker than the normal femur and quite different in shape, (fig. 10 *fe*.) In place of the nearly spherical ball which forms the proximal end of the normal femur, this cartilage articulates with its girdle by an elongated knob which is thick posteriorly and gradually tapers off toward the front. An enlargement at the middle of its posterior surface gives this femur the appearance of being arched backward. It is of about the same size throughout its entire length. At its anterior end it articulates ventrally by a large surface with the tibia (*t*) and dorsally just touches the end of the fibula (*f*). From this joint to the distal end of the foot the process of chondrification is still incomplete. The outlines shown in fig. 11 must therefore be looked upon as indicating centres of chondrification rather than clearly defined and fully developed cartilages.

The tibia and fibula present nothing of particular interest. They are shown in outline fig. 11.

The tarsus is composed of ten cartilages; a tibiale, (*ti*), a fibulare (*fi*), an intermedium (*in*), three cartilages lettered c^1, c^2 and c^3, and interpreted as representing the centrale, and four tarsales, numbered 1 to 4, lying at the base of the digits bearing the corresponding Roman numerals. The unusual length of the fibulare may be accounted for by assuming that its distal part is composed of the missing tarsale 5. The intermedium is as

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long as the fibula and has the appearance of being composed of two parts overlapping each other at their ends, a condition not shown in the outline drawing. Of these two parts the posterior is lateral in position; that is, it lies nearer the dorsal surface of the tarsus, while the anterior part is median, or towards the plantar surface of the tarsus. Tarsale 1 is exceptionally large and roughly cylindical in shape. All of the other components of the tarsus not especially mentioned above are small and approximately spherical or ovoid in shape. The occurrence of centrales to the number of three and even four has been noted by Zwick ('97), Wiedersheim ('80) and others. The following statement by Wiedersheim ('80, p. 582) is very interesting in the light of the preceding description. He says, "Das ungemein häufige Vorkommen eines mehrfachen Centrale deutet überdies darauf hin, dass die Zeit vielleicht noch gar nicht weit hinter uns liegt, in der jeder Axolotl *constant* ein doppeltes oder dreifaches Os centrale besessen hat. Es wäre interessant bei den Larven der amerikanischen Amblystomen hierüber Beobachtungen anzustellen." It is stated by Howes and Ridewood ('88, p. 177) "that the living Anura are unique, as an Order, in the invariable possession of two large centralia carpi."

Digits I and V consist of a single joint each; digit IV has two joints; and II and III each have three joints. The contrast between this condition and that found in the normal adult individual is best shown by the following table.

Digit	I	II	III	IV	V
Number of joints in normal individual	2	3	4	5	3
Number of joints in abnormal individual	1	3	3	2	1

The relative lengths of the digits are shown in fig. 11.

The differentiation of the muscular tissue has not proceeded far enough to enable its separation into a series of individual muscles which can be compared one by one with those occurring in the normal leg of an adult Amblystoma. But there are here seven quite well-defined masses of muscle shown as reproduced in the model in figs. 12 and 13 and in sections in figs. 15 to 20. They have been designated by the heavy type letters *A* to *G*

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In figs. 12 and 13 the general directions of the muscle fibres is indicated by the shading lines.

A is a differentiated portion of the muscle of the body wall in which both its ends lie. Its ventral end is near the median line of the body, just inside the pubic cartilage of the abnormal girdle. From here it runs dorso-laterally over the end of the girdle and terminates among the fibres of the lateral plate. There is no muscle in the normal animal corresponding to this one. *B* is a large sheet of muscle arising from the dorsal and postero-lateral surfaces of the pubis and ilium. It extends forward along the posterior and dorsal surfaces of the femur and by a thin dorsal portion reaches the fibula. It may be considered to represent the ileo-extensorius, the ileo-femoro-fibularis and the ileo-femoralis, using the nomenclature of Hoffmann. *C* is a rather broad and thin muscle arising from the dorsal surface of the anterior end of the femur and inserted along the ventro-lateral surface of the tibia. It may be compared to the normal femoro-tibialis. *D* is a large and thick mass of muscle which arises from the ventral surfaces of the ischium and pubis, and inserts upon the ventral surfaces of the femur, tibia and fibula. It occupies the position of the normal ischio-flexorius, pubo-tibialis, pubo-fibularis, and pubo-ischio-femoralis-externus. *E* is a muscle arising from the median surface of the fibula and inserted upon the ventral surface of the tibia. Its action would seem that of a pronator. *F* is a long slender muscle arising from the ischium and inserted upon the tibia in company with the fibres of muscle *E*. These two muscles last mentioned have little similarity to any of the normal muscles. *G* is a short and thick muscle having its origin upon the lateral surfaces of the ischium and ilium and inserted upon the dorso-median surface of the femur. It bears considerable resemblance to the normal ischio-femoralis. There are several smaller bundles of muscle fibres in the more distal parts of the leg but their relations to the cartilages are too uncertain to justify a description.

One of the most interesting features about this abnormal appendage is the small U-shaped branch of the intestine which extends into it. Fig. 14 is a drawing of this structure as it

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appears in the model. Sections through this region are shown in figs. 15 to 20. As represented in fig. 14 this branch of the intestine passes out from the side of the otherwise normal intestine a short distance in front of the abnormal pelvic girdle. It immediately bends backward and runs parallel with the normal intestine as far as the abnormal girdle, becoming gradually larger. Here it turns nearly at a right angle, passes below the ilium into the leg and, again bending, extends forward along the dorsal surfaces of the femur and fibula to the region of the tarsus where it opens to the exterior by a minute vent (figs. 14 and 20 *vt*) just above the fibulare. The total length of the intestine measured from the opening in the normal intestine (*in*) through the centre of the tube to its vent is two and one fourth millimetres. Its greatest diameter, at the second bend, is about four tenths of a millemetre. The form and relative size of the lumen is indicated by the dotted lines in fig. 14.

At the second bend, just as it passes into the leg, there is an enlargement. Then follows a constriction and another enlargement, after which it gradually tapers off to the very small vent. At the first enlargement the lumen also undergoes a corresponding increase in size, while at the second enlargement the central cavity is only slightly increased but several minute tubules pass out from it towards the outer surface of the intestine. These features suggest that we have here an epitomized and incomplete alimentary canal with an enlargement for a stomach and a tubular portion representing some of the normal intestinal glands. The minute size of the structure and the fact that the inner end of the lumen was practically closed precludes the possibility of its taking any part in the digestive processes.

Owing to some imperfections in the sections and the absence of blood from the artery or arteries supplying this leg, I was unable to trace out this system of vessels. The veins, however, were sufficiently distended to allow the plotting and reconstruction of their proximal ends. The result is shown in fig. 21 which represents somewhat diagramatically the veins of this region as seen from the dorsal aspect. The abdominal vein (*av*) is normally formed by the union of two lateral veins (*lv*) each of which comes from the corresponding iliac vein (*iv*).

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Into this lateral vein empties a cutaneous vein (*cv*) running backward along the side of the body. These normal veins are all present in this specimen and in addition to them there is a plexus formed by a number of small veins which connect the abdominal with the cutaneous vein, fig. 21. As will be seen from this figure there is not a single large iliac vein in the abnormal leg as in the normal leg but all the blood is conveyed by smaller vessels. Three abnormal vessels, v^1, v^2, and v^3, enter the right side of the abdominal vein. The first of these, v^1, comes directly from the cutaneous vein; v^2 and v^3 are two veins which have a common origin in the cutaneous vein just in front of the origin of v^1. Two small veins from the leg, x^1 and x^2, empty directly into the cutaneous, and two others, y^1 and y^2, empty into v^3.

The normal sacral plexus in Amblystoma is composed of nerves arising from three ganglia, those included between the fourteenth and the seventeenth vertebræ. From it come an obturator, a crural, an ischiadic and a caudal nerve, and one or more nerves to the body wall. Corresponding with the two appendages in this region, there is in this specimen a compound sacral plexus (fig. 22), the posterior half of which innervates the normal leg and the anterior half the abnormal leg. For convenience of reference, the five ganglia entering into the composition of this plexus have been indicated by the heavy type letters *R* to *V*. As will be seen by reference to the figure, the posterior half of the plexus is entirely normal. Ganglia *T*, *U*, and *V* are involved in it, and there are two nerves to the body wall (*mn* and *mn'*), an obturator (*on*), a crural (*cn*) an ischiadic (*isn*), and a caudal nerve (*ca*). The abnormal portion of the plexus is formed by ganglia *R*, *S*, and *T* and nerves coming from them. Thus ganglion *T* is seen to contribute nerves to both the normal and abnormal portions of the plexus. Corresponding with the position of the abnormal leg, the order of the nerves in the anterior portion is the reverse of that in the posterior. There are here an obturator (on^1), a crural (cn^1), and an ischiadic nerve (isn^1), and three nerves to the body wall (mn^{2-4}), one of which (mn^3) may be said to correspond to the normal caudal. The relations of the obturator and crural nerves

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in the two portions of the plexus differ somewhat, and the ischiadic nerve of the normal leg is much larger than that of the abnormal. Yet the similarity between the two portions of the plexus is quite striking, especially when we take into account the frequent large variations which Adolphi ('93, '95, '96, '98 and '02) and others have shown to occur in corresponding plexuses of Urodeles normal in other respects. It will be seen, therefore, that in the nervous system we have an expression of the symmetry characteristic of repetition of parts in mirror-like image quite as pronounced as that externally apparent.

LITERATURE AND DISCUSSION.

The above described specimen (Case 3) has theoretic value from its bearing upon the problems of variation in the length of the presacral region and of asymmetrical sacra. These problems have attracted the attention of many investigators who have presented a number of theories based upon studies of a great variety of organs in species covering the whole range of Vertebrates from the Amphibia to Man.

Without attempting an exhaustive review of the discussions to be found in the literature upon this subject we may consider the theories advanced as four in number, constantly recognizing that the acceptance of one of these as the true explanation of certain cases does not necessarily exclude the acceptance of others for other cases; and also recognizing that so brief a statement of a theory as that here attempted must be incomplete and cannot take account of minor shades of opinion.

1. *The theory that variations in the length of the presacral region are due to a movement of the pelvis along the spinal column, and that asymmetrical sacra result from an inequality of movement on the two sides of the body.*

This proposition has been best set forth and defended by Rosenberg ('76 and '99). Studying human embryos and the adult skeletons of some of the monkeys and apes and of man, he came to the conclusion that both ontogenetically and phylogenetically there has been a forward movement of the pelvic girdle with relation to the vertebral column. He finds that in man at different stages the sacrum is composed of morphologically dif-

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ferent components; namely, in the earlier stage vertebræ 26 to 30, and in the later stage vertebræ 25 to 29. On this basis he interprets a reduction in the number of presacral vertebræ as a progressive step and an increase in this number as a case of atavism. There is implied in this view the permanence and individuality of the different vertebræ as opposed to the idea of Welcker, Bateson and their followers, that there is no strict homology beween the individual members which occupy the same position numerically in two Meristic Series when the total number of members in the two series is different.

Wide acceptance has been given to this theory and a large amount of evidence of a more or less directly confirmatory nature has been adduced in its support. Solger ('76) and Fürbringer ('79) were among its first adherents, the latter, as he tells us (p. 326), accepting this view even at the expense of giving up the the theory of 'intercalation' which he had previously held. Claus ('76) also came out with an important paper in full accord with this view.

Paterson ('89, p. 298) states his conclusion as follows: "The position of the hind-limb is less constant. While it may retain its embryonic position, in most cases it displays a tendency to move backwards. (This agrees with Gadow's conclusion in regard to birds)."

Baur ('91), while devoting his attention chiefly to an argument for intercalation, says (p. 331), "Cases of the movement of the sacrum have very often been described, and quite a number have come under my own observation."

Eisler ('92), studied the human lumbosacral plexus and came to the same general conclusion with Rosenberg and Fürbringer. On page 350 he says, "Der 10. Wirbel des einen Thieres ist Homolog dem 10 des andern."

From his studies of Pipa and Xenopus, Ridewood ('97, p. 366) concludes that "When variation in the number of presacral vertebræ does occur, the explanation is to be sought, not in the intercalation or excalation of vertebræ, which, as Parker ('96, p. 715) has already pointed out, are to be looked upon as very rare occurrences, but rather in the shifting of the

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ilium forwards or backwards on to the vertebra in front of or behind the normal."

Adolphi ('98, p. 553) says, "Es ist hier so recht deutlich zu sehen, wie viel besser die Hypothese Rosenberg's den Thatsachen als die Hypothese Welcker's." Also ('02, p. 375) "*Das Sacrum und die obere Thoraxgrenze verschieben sich demnach hier in der gleichen Richtung.*"

Dwight ('01, p. 310) gives a partial acceptance but invokes the 'vital principle' as an *explanatory* cause.

More important than any of these, however, *if true*, is the work of Credner ('86), who claims that in the ontogeny of the Stegocephalan *Branchiosaurus amblystomus* Cred., the pelvis moves backward through six or seven segments. The basis for this very remarkable assertion is found in a graded series of fossils, in which the presacral region varies from 19 to 56 millimeters in length. In the shorter (younger) individuals there are 20 presacral vertebræ, and in the longer (older) individuals the number of presacrals gradually increases to 26 or 27, as shown in the following table (Credner '86, p. 620); —

Length of Vertebral Column from Posterior Border of the Skull to the Anterior End of the Sacral Vertebra in millimeters.	Number of Presacral Vertebræ.
19	20
23	20
25	20
26	20
27	20
28	21
30	21
32	21
33	21
37	22
39	23 or 24
43	25 or 26
48	25 or 26
50	26
52	26
54	26 or 27
56	26 or 27

This is mentioned by Baur as "the highest number of sacral

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variations that has been observed." Granting, as Credner claims, that these represent different stages in the ontogeny of Branchiosaurus, we must admit that this is a demonstration of the theory under discussion.

In what appears to be a very careful embryological study of the lumbosacral region of man, Holl ('82) disagrees with Rosenberg both as to observations and conclusions, and argues (p. 221) that as a whole the vertebral column of one animal is homologous with that of another, and not with two-thirds or three-fourths of it. Bateson regards this solution of the problem as an inaccurate use of language. He says ('94, p. 111), "In describing cases of such transformation in the series, it is usual to speak of structures — the pelvis for example — as 'travelling forwards' or 'travelling backwards.' These modes of expression are to be avoided as introducing a false and confusing metaphor into the subject, for there is, of course, no movement of parts in either direction, and the natural process takes place by a development of certain segments in the likeness of structures which in the type occupy a different ordinal position in the series."

2. *The theory that variations in the length of the presacral region and asymmetrical sacra are the result of the intercalation or excalation of one or more whole or partial vertebræ.*

According to Welcker ('78, p. 291) this theory was first advanced by H. v. Ihering ('78 and '80). It was accepted, and later largely rejected, by Fürbringer, as stated above, and it was accepted by Albrecht ('83). For convenience I quote Baur ('91, p. 332) upon this point. "Albrecht examined a skeleton of *Python sebæ* in the Museum at Brussels. Between the 194th and the 197th vertebræ, he found a complex of anchylosed vertebræ; this contained on the right side two vertebral elements, one foramen intervertebrale and two ribs; on the left side three vertebral elements, two foramina intervertebralia, and three ribs. Albrecht considers the supernumerary vertebra on the left side as intercalated."

As the most vigorous exponent of this theory, however, and the one to apply it with the widest range, we must turn to Baur ('91 and '97). In his earlier paper he mentions specimens de-

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scribed by Albrecht, Owen, Koken, and himself, and says of them (p. 333), "I do not doubt at all that in all these cases we have examples of incomplete intercalation; and I am convinced that this intercalation is the result of the division of the myotomes, as expressed by Albrecht." He then proceeds to the description of a specimen of *Gavialis gangeticus*, which has a "new vertebra" "intercalated between the ninth and tenth," and later (p. 335) says, "*My opinion is that in the increase of the number of segments not only in vertebrates, but also in invertebrates, intercalation has played a much greater rôle than is generally admitted.* At the same time I admit addition of segments at the distal end, as well as occasional *slight* migration of the shoulder girdle and pelvis in both directions."

In discussing this problem Parker ('96, p. 715) says, "Baur ('91, p. 331) in a recent article, has shown very conclusively that, in place of one vertebra, two, or parts of two, may arise, the process evidently being a partial division of the material from which a single vertebra ordinarily arises. This process, which I should call the multiplication rather than the intercalation of vertebræ, may in some cases account for the increase of presacral elements, but I am not inclined to ascribe to it the wide-spread importance that Baur does."

The opponents of this theory, at least in so far as granting it any but a very insignificant place, seem to be more numerous and more vigorous than its supporters. Paterson ('93, p. 194) says that it fails "to meet the case." Bumpus ('97, p. 478) says, "The sacrum, pelvis, and appendages are not intimately associated parts of the body that represent one complete whole, and the difinitive location of the sacrum is probably due to centripetal influence derived from the budding appendage. *Intercalation in the sense of the introduction of a new segment does not take place, and what have been given as examples of intercalation are probably only imperfectly formed body segments.*" Among others who have argued for the insufficiency of this theory we may mention, without quoting further, Welcker ('78), Ruge ('92), Bateson ('94), Waite ('97), and Ridewood ('97).

3. *The theory that variations in the length of the presacral region are due to* * "*an initial variation in the serial number and position of centres of metamerism.*"

* Waite

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This theory was advanced by Welcker ('78), but has been much more fully expounded by Bateson ('94). No attempt is made to explain asymmetrical sacra by this theory alone, but it is regarded by its advocates as offering the only admissible explanation for such variations as that between the pigeon's neck with 15 vertebræ and the swan's with 26, and the similar case of the necks of the Plesiosauria mentioned below. This conception necessitates the giving up of the idea that the individual members of one Meristic series are strictly homologous, with the members of another series occupying the same numerical position, when the total number of members in the two series differs. Bateson's discussion of this theory is so well known and so important, that it would be an unnecessary repetition to go into it further here. I wish, however, to call attention to a passage of very particular interest from Baur's paper of '97; first, because it illustrates this theory so well, and, second, because of the use to which Baur has put it. He writes (p. 52), "The increase of the number of cervical vertebræ in the Plesiosauria is certainly not produced by a shifting backwards of the shoulder girdle, but by the addition of new vertebræ by intercalations, as will be seen from the following table: —

PLIOSAURIDAE	Cervicals	Dorsals	Sacrals	Caudals
Pliosaurus evansi Seeley	19–20			
Peloneustes philarchus Seeley	20–21			
PLESIOSAURIDAE				
Plesiosaurus rostratus Owen	28	20	2	34
Plesiosaurus macrocephalus Owen	30	20	2	18+*
Thaumatosaurus megacephalus Stutchbury	30	26	2	34
Plesiosaurus hawkinsi Owen	31	23	2	—
Cryptoclidus oxoniensis Phillips	31	23	2	23+
Plesiosaurus guilelmi-imperatoris Dames	35	20	2	37
Plesiosaurus conybeari Sollas	38	21	2	5
Plesiosaurus homalospondylus Owen	38	22	2	25+
Plesiosaurus dolichodeirus Conybeare	41	21	2	30+
Muraenosaurus plicatus Phillips	44			
ELASMOSAURIDAE				
Elasmosaurus platyurus Cope	72	20	2	23+

* + means that the tail is not completely preserved.

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Everybody who will examine this table must admit that the increase of the number of cervical vertebræ can only be explained by intercalation. We see, therefore, that intercalation really occurs."

It is difficult to understand how such a statement as this last could be made by one familiar with Bateson's work, as Baur must have been, except on the assumption that the writer's predilection for the term intercalation was so great that he chose to retain it as the name for a process which is clearly different from that which he and others have usually designated by intercalation. No better illustration of Welcker's theory can be found than this table of Plesiosauria and I cannot believe that Baur failed to recognize the true nature of the process involved in spite of the fact that he calls this also intercalation. This only serves to emphasize, what I shall state more fully below, that there is a close resemblance between intercalation as used by Albrecht and Baur and an initial variation as described by Welcker and Bateson.

Besides the two last mentioned writers, this theory has been at least favorably considered by Parker, and accepted by Howes and Dwight. Waite ('97) offers pertinent criticism upon it as applied to his studies on the Plexi of Necturus as follows (p. 85)

"While the idea of variation in the number and position of centres of metamerism may be attractive on theoretic grounds, it has no observational evidence to support it, and, further, is insufficient to account for unsymmetrical sacra and supernumerary sacral ribs."

Not finding any of the above three theories satisfactory for their cases of variation in Necturus, Parker ('96) and Waite ('97) have advanced

4. *The theory that variations in the number of presacral vertebræ and asymmetrical sacra are due to the fact that* (Parker, *p. 176*) "*the sacral region has the power of developing sacral ribs*" *and pelves* (and Waite) "*at several points on both right and left sides.* Such an assumption is by no means unnatural, for it offers an easy explanation both for the appearance of symmetrical sacra on the twentieth in place of the nineteenth vertebra and for the occurrence of unsymmetrical sacra. It also implies that an

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animal may possess more than one sacral rib on a side, which might be taken as an objection to this hypothesis, had the actual occurrence of such cases not already been demonstrated by Huxley ('75, p. 752) and by Lucas ('86, p. 562) in Menopoma."

Waite's conclusions are as follows ('97, p. 86):—"It is more logical to consider that the new position of the girdle is due to a stimulus to girdle formation having been applied at a *new* point, i. e. in a segment other than the normal, and hence that a sacral rib may arise in any one (or more, as shown in supernumerary ribs) of several points in this region. In Necturus these points are at least three, located in the 18th, 19th, and 20th segments." And, "From the foregoing discussion I conclude that *neither intercalation or excalation, nor slipping, are involved*, but that the abnormal position of the girdle represents development of a new girdle at a new point."

It is right here that my specimen (Case 3) is of interest, showing as it does in an indisputable manner that two appendages, including the girdles, may be produced instead of the one of normal animals, thus, in a way, completing the evidence presented by Parker and Waite. Huxley and Lucas have reported cases with two sacral ribs; Parker, Waite and others have described pelves attached to three different vertebræ, symmetrically and asymmetrically, and in the above specimen we have two appendages, one of which is normally attached and the other free, i. e., with no sacral rib, probably on account of the distance separating the abnormal ilium from the spinal column. Very little remains to be desired to prove the truth of the proposition that sacral ribs and appendages may arise at any one of several points, resulting in variations in the length of the presacral region and in asymmetrical sacra.

In accepting this theory it is obviously necessary to recognize the fact that ordinarily only one of those segments which are potentially able to produce an appendage does so. Or, to put it in another way, normally the stimulus to appendage formation is single, but in these rare cases of abnormality it is double and there results a duplication of parts. It should also be noted that the idea that there are several points on the side of the body capable of producing an appendage is, in a way, a

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corollary of the facts discussed by Bateson under the head of Homeosis, for, in saying that a segment may assume the form of the segment in front of or behind it we practically say that the segment has in itself potentially the qualities which are normal to the two adjacent segments.

We thus have four explanations for variations in the length of the presacral region, none of which applies in all cases but each of which renders some cases more intelligible. It is also clear that these four different methods of producing one result are not in all cases entirely unlike. Particularly is this true of 'intercalation' and an 'initial variation in centres of metatamerism,' for the first term as commonly used designates a division of the material which ordinarily forms one segment into two segments,—a localized process—, while the second expression is used to designate the same *kind* of a change but one acting through a considerable number of segments, for example, the cervical region. It may be argued that those cases which are referred to as showing initial variation, such as the necks of the Plesiosauria are simply a gradual accumulation of intercalations by inheritance. Such a contention, however, only adds to the confusion, whereas for the sake of clearness it is much preferable to use the terms with the generally accepted limitations above stated.

In discussing the theory of the slipping of the pelvis in the preceding pages I have assumed that the writers mentioned used the word 'slipping,' 'verscheibung,' or its equivalent with its proper significance, for we must surely grant this to be the case with Credner. It is to be regretted that this assumption is not well founded, for in many instances it is evident that instead of a real *movement of the pelvis* there has been either an initial variation or a development of the appendage in a segment other than the normal. That this inaccurate use of language should continue after having been pointed out by Bateson is inexcusable and very unfortunate.

Very little value can be attached to an attempt closely to limit the application of these four theories in the present imperfect condition of our knowledge. Until Credner's conclusions are verified and other writers who describe movements of

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the pelvis use language which is unmistakable, many will doubt whether there *is* such a process, choosing rather to class the variations called by this name under one of the other three heads. Intercalation, *in the sense used by Albrecht*, is, without doubt, a real process though a rare one even among variations which result in a change in the number of segments in the animal as a whole or in some particular region. But by far the greater number of such variations are best explained by the third or the fourth theory.

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EXPLANATION OF PLATES.

Fig. 1. Outline of Amblystoma foot with bifid toe.

Fig. 2. Outline of bifid toe showing the bones.

Fig. 3. *Plethodon glutinosus*, with bifid tail.

Figs. 4 to 8. Sections of the same.

Fig. 9. *Amblystoma punctatum*, with a fifth leg.

Fig. 10. Ventral view of the girdle, femur, tibia and fibula of the abnormal leg.

Fig. 11. Outlines of the cartilages in the lower leg and foot as seen from the dorsal surface.

Fig. 12. Postero-dorsal view of model showing position of muscles *a'*, *b*, and *c*, and the abnormal intestine.

Fig. 13. Ventral view of model showing muscles *a*, *b*, *d*, *e*, *f*, and *g*, and the abnormal intestine.

Fig. 14. Dorsal view of parts of dissected model showing abnormal intestine, with dotted lines to indicate the course of its lumen, and with dotted transverse lines to show the position of the sections shown in Figs. 15 to 20.

Figs. 15 to 20. Sections through abnormal leg. See fig. 14 for position of sections.

Fig. 21. Dorsal view of a reconstruction of the veins coming from the abnormal leg.

Fig. 22. Diagram of the spinal column, a reconstruction of the nerve-plexus, and the normal and abnormal pelvic girdles.

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REFERENCE LETTERS.

a, abnormal leg.
a to *g*, (larger type), muscles of abnormal leg.
av, abdominal vein.
c^1, c^2, c^3, components of the Centrale.
ca, caudal nerve.
cn, crural nerve.
cn', abnormal crural nerve.
cv, cutaneous vein.
f, fibula.
fe, femur.
fi, fibulare.
i, normal intestine.
i', abnormal intestine. In figs. 13 and 18 the accent has been lost from the *i*.
il, normal ilium.
il', abnormal ilium.
in, intermedium.
is, normal ischium.
is', abnormal ischium.
isn, normal ischiadic nerve.
isn', abnormal ischiadic nerve.
it, intestinal tubules.
iv, iliac vein.
lm, lateral muscle plate.
lv, lateral vein.
m, entrance to abnormal intestine.
mn to mn^4, Nerves to lateral muscle plate
n, notochord.
o, outline of body.
oa, outline of abnormal leg.
of, normal obturator foramen.
of', abnormal obturator foramen.
on, normal obturator nerve.
on', abnormal obturator nerve.
p, abnormal pelvic girdle.
pn, normal pubis.
pu', abnormal pubis.
r, sacral rib.
r-w (large type), ganglia forming sacro-sciatic plexus.
s, skin on tarsus.
sc, spinal cord.
t, tibia.
ti, tibiale.
tm, anterior transverse muscle.
tm', posterior transverse muscle.
v, vertebra.
v^1, v^2, v^3, veins of the abnormal plexus connecting *av* with *cv*.
vt, vent of abnormal intestine.
x^1 and x^2, veins of abnormal leg emptying into cutaneous vein.
y^1 and y^2, veins of abnormal emptying into v^3.
1 to 4, tarsales one to four.
I to V, phalanges.
15 to 20 in fig. 14. See Explanation of fig. 14.
12 to 18 in fig. 22. Vertebræ.

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THE HISTOLOGY OF THE DIGESTIVE TRACT OF AMBLYSTOMA PUNCTATUM.

By George A. Bates.

Most of the histological work upon the Amphibia has been done upon the frogs and upon the lower members of the group, Proteus and Necturus. This paper is the result of studies begun with the idea of working out the development and histogenesis of the digestive tract in one of the Salamandrina, a knowledge of the adult conditions being found necessary for the understanding of the earliest stages. The writer has been somewhat hampered by the difficulty of obtaining material, the burrowing habits of the adult making it difficult to find the animals except in the spring, at the time of laying the eggs.

The digestive tract falls naturally into five divisions, — oro-pharyngeal cavity, œsophagus, stomach, intestine and cloaca, — which are described below (fig. 1). No attention was paid to the accessory digestive organs — pancreas, liver, etc. — except as the description of the course of their ducts made it necessary.

The Oro-Pharyngeal Cavity.

This cavity extends from the external opening anteriorly to the anterior end of the œsophagus posteriorly. Upon the floor lies a fleshy tongue, which is attached along its entire length. The cavity is broad in front, and narrows gradually at the posterior part. The entrance to the œsophagus is quite abrupt. At the base of the tongue the floor is thrown into a series of longitudinal folds, which are continuations of like folds in the ventral wall of the œsophagus.

The surface epithelium is stratified, the upper layer of cells being cubical, or columnar. These cells bear a stripe on their free border, and everywhere, except on the dorsum of the tongue, they are ciliated, as in figs. 2, 6 and 9. It differs in this respect from Necturus, in the mouth of which Kingsbury found no cilia, a condition which probably holds with all the aquatic

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forms. Goblet cells (fig. 16*a*) are everywhere present, often occurring in groups.

The ciliated columnar and goblet cells are in many places intermingled. This is true particularly of the folds in the mucous membrane at the sides of the tongue. The columnar cells are trumpet-shaped, the broad ends being uppermost where they come together, leaving oval spaces between them that are occupied by the goblet cells (fig. 2). A surface view shows the goblet cells opening among the columnar forms, which seem to be arranged in circles around the openings.

The height of the surface cells varies according to situation. At the sides of the tongue and at the angles of the mouth there are, in the stratified epithelium, many layers of cells. Here the surface cells are tall, and assume many peculiar shapes (fig. 17*a*, *b*), the difference apparently being due to unequal pressure. The underlying cells are small rounded polygonal forms (fig. 12*b*), and are frequently seen in mitosis. In many cases there appear small depressions, or pits, in the mucous membrane, which suggest tubular glands (fig. 3). The cells which line these depressions do not usually differ from the surface forms, except in the loss of their cilia (fig. 3*a*). Some of the deeper pits have goblet and columnar cells intermingled.

The blood supply of the epithelium is found in the submucous layer, and is very abundant, the capillaries, in many instances, seeming to penetrate among the surface cells much as has been described by Maurer in the frog. Among the epithelial cells were seen many which had vacuoles containing leucocytes (figs. 2, 9, and 16*b*). These cells were found in the epithelium throughout the entire length of the digestive tract, and will be discussed later.

At the base of the tongue, just at the junction of the mouth cavity and the anterior end of the œsophagus, occur numerous structures formed by the infoldings of the epithelial surface which penetrate into the underlying connective tissue. They seemed, at first sight, to be extensions of the folds of the ventral wall of the œsophagus. Tracing them through serial sections, however, demonstrated them to be tubular in form at the surface end, becoming more or less sacculated in the deeper parts.

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They were lined by large, clear cells. At the inner extremity these cells are massed together, the masses being penetrated by the lumen, which branches a short distance from the surface, giving the structure the sacculated appearance. Here and there appear groups of goblet cells (fig. 5). Among the cells lining the lumen occur large, clear forms having the characteristic reticulated structure in the cytoplasm, which distinguishes the mucous cell (fig. 15).

Passing forward these structures become more numerous, assuming more and more the character of tubular glands. When the anterior extremity of the tongue is reached they are thickly crowded, extending from the dorsal surface through the entire thickness of the organ. For a short distance from the surface they are straight, but become tortuous as they penetrate more deeply into the body of the tongue. The tubes are lined with large clear cells, some of which closely resemble goblet cells. In the inner portion of the tube the cells become changed, assuming the character of true gland cells. Their cytoplasm is filled with zymogen granules of some sort and, in my preparations, these bodies were clustered about the lumen of the tube, leaving the basal portion of the cell clear. The cells very much resemble those of the parotid gland and pancreas in the higher vertebrates (figs. 4, 4*a* and 11).

The granules found in these cells bear a close resemblance to the zymogen granules of the pancreatic cell. This offers a suggestion that the granules in this place may be the zymogen of some enzyme which may furnish an element to the digestive fluids.

Oppel, in his investigations on Proteus, does not mention these glands and, in his figure of a cross-section of the mouth, does not show them. I therefore infer that they do not occur in that form. Oppel says "Aside from the goblet cells the mouth possesses no secreting cells, much less glands." Kingsbury, in his work on Necturus, makes no mention of these structures. I have sectioned the frog tongue and find the glands present.

These glands are evidently partly mucous in character, but the peculiar granulated cells of the lower portions of the gland tubules suggest some secretion other than mucus. They are

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probably stimulated by the presence of food in the mouth, furnishing a lubricating fluid which acts as an aid in the process of swallowing and possibly an enzyme as well. To one who has seen one of these animals swallow a worm nearly as long as his own body, one function of these structures is at once apparent. Numerous masses of voluntary muscle occur among the gland tubules, which would suggest that the tongue is possessed of some functional movements. In this connection Oppel says of Proteus, "the tongue contains no muscle, only connective tissue and fat." In the submucosa of the tongue is found a very abundant blood supply, the capillaries coming into very close relations with the glands and epithelial surface.

No sense organs, such as are described by Kingsbury in Necturus, were found.

THE ŒSOPHAGUS.

The œsophagus extends from the base of the tongue to the stomach. Its walls are characterized by the longitudinal folds which are more pronounced at the anterior extremity.

The epithelium consists of ciliated columnar and goblet cells. The columnar cells in the anterior end of the tube are inclined to assume a trumpet-shape, enclosing the goblet cells covering the surface of the mouth cavity. This condition changes in the part of the organ nearest the stomach. Here the columnar cells become straighter and more uniform, while the goblet cells are less numerous and often appear with masses of mucus protruding from their free ends (fig. 19). Among the columnar cells is often seen a form which is more or less spindle-shaped. These are closely packed among the columnar cells, often bearing marks of adjacent cell bodies upon their protoplasm. Under the surface cells occur several strata of rounded polygonal cells. These are the substitution cells. The nuclei of the various cells of the epithelium occupy different levels, making the characteristic structure of stratified columnar epithelium. Just before the œsophagus reaches the stomach, the goblet cells are much less numerous and the surface epithelium consists entirely of the columnar ciliated forms (fig. 8.) Here and there a cell still preserves its trumpet-shape, but for

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the most part they are typical in shape with oval nuclei. Among the epithelial cells throughout the entire length of the organ were found vacuoles containing leucocytes.

Outside the epithelial layer, the œsophagus has a well-marked submucosa of connective tissue, but a muscularis mucosæ could not be demonstrated. The usual arrangement of muscle layers: an inner circular, and an outer longitudinal layer is present. Of these, the inner circular is the thicker. This muscular tissue is involuntary in the lower part of the tube, but voluntary in the upper portion. In the latter portion the outer layer seems to be wanting.

In Necturus Kingsbury found, at the junction of the œsophagus and stomach, a form of sacculated gland which he thought might be homologized with the œsophageal glands of the frog, as described, first, by Bischoff in 1858 and, later by Langley. Oppel, in his paper on Proteus, figures such glands and calls them "œsophageal glands." He shows how they differ under conditions of fasting and full feeding. No such glands were found in Amblystoma. Kingsbury sectioned Diemyctylus and found these structures wanting. According to the researches of Bensley such glands are developed in the œsophagus of the larva of Amblystoma and are subsequently modified into oxyntic glands and included in those of the anterior end of the stomach. May this not account for the peculiar many tubed form of gland described by Klein for Triton, Langley for the frog, and found by Kingsbury in Necturus?

At the point where the œsophagus enters the stomach were seen the glands, composed entirely of large clear mucous cells, found in Necturus by Kingsbury and thought by him to be developed from the surface epithelium by infolding. They seemed to form a ring around the stomach end of the œsophagus, and were separated from the stomach by connective tissue, opening upon the surface among the ciliated cells. Klein described these glands for Triton, and questions whether they may not be homologous with the œsophageal glands of the frog (figs. 27 and 45.)

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THE STOMACH.

Externally there is no perceptible line of demarkation between the œsophagus and stomach. The former becomes a free tube as it leaves the mouth cavity, of which it is a continuation, becoming abruptly narrower at this point. As it approaches the stomach it gradually broadens, passing imperceptibly into the latter organ. This is true of the empty stomach. When it is distended with food, the anterior end is much larger and the line between the two organs much more apparent.

Internally the line of distinction is very marked. It cannot however be said that the change in structure is very abrupt, as in the case of the higher forms where the stratified pavement of the œsophagus is suddenly changed to simple columnar epithelium of the stomach, for here the columnar form of cell characterizes both these divisions of the enteron. The change is more or less gradual, the ciliated cells of the œsophagus mingling with the mucous cells of the stomach, and yet it is abrupt enough to mark the line where one ends and the other begins (fig. 7).

The epithelium of the mucous surface of the stomach is composed of the peculiar columnar mucous cells, so characteristic of all the forms of Amphibia. The cell is broad at its free end and tapers to its attached extremity. The nucleus is large and oval and situated, in some cells, at the inner third of the cell and, in others, well toward the free end. There seems to be several strata of nuclei, giving the epithelial tissue the appearance of being stratified. At the outer end of the cell, masses of mucus are seen protruding (fig. 45 *b*). On the surface, the cells are tall and shapely; in the necks of the glands and on the sides of the folds of the mucous membrane, they are very irregular in shape as may be seen in figs. 23, 27, and 28. In many cells a stripe may, with more or less difficulty, be made out. The cytoplasm is very granular. Kingsbury, in his studies of the stomach of Necturus, claims to have demonstrated these granules to be fat. This seems to the writer to be impossible, for reasons which will be presented later.

The most important structures in the stomach are the glands. They are tubular in form and composed of two kinds of cells,

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viz.:—a large clear mucous cell, which appears in groups at the end of the gland towards the neck; and, attached to this group and projecting from it towards the lumen of the organ, are two or more tubular structures composed of smaller, polygonal granular cells. These two forms of cells, together, form the gastric glands (fig. 28 *b*, *c*).

There are no cardiac and pyloric regions distinctly marked off by the character of the gland as in higher forms, nor is there a transitional area. The glands grow shorter and fewer in number as the pyloric end of the stomach is approached, and the clear mucous cells become less numerous until they cease altogether at the posterior fourth of the organ. The gland tubes are embedded in a basement membrane of connective tissue. which brings to them their blood supply. Between this structure and the fibrous coat occurs a well-marked muscularis mucosæ, composed of an inner circular and an outer longitudinal layer of involuntary muscle tissue. The fibrous coat is formed by a thick layer of connective tissue, in which the large vascular trunks are located. Outside this, the usual musculature, consisting of an inner circular and an outer longitudinal layer occurs.

The mucosa of the stomach is thrown into a series of longitudinal folds, five in number. Two folds on each side project laterally into the lumen. Ventrally there is no fold, the wall being occupied only by small villi-like projections. These folds are gradually reduced toward the pylorus. In the process of reduction, the two left lateral folds are the first to be affected; after which the corresponding right folds are acted upon,—the dorsal one being first reduced, while the ventral one takes its place opposite the dorsal fold. In this way the persisting folds come to be nearly dorsal and ventral. The dorsal fold is now reduced while the ventral one persists and passes a short distance into the duodenum.

In the epithelium, both in the cement substance between the cells and in the cytoplasm of the cell body, there appeared many vacuoles containing leucocytes. In the submucous coat at the base of one of the mucous folds, was discovered a very large vacuole. It was traced through fourteen sections, giving it a

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length of 140 microns, while careful measurement gave it a diameter, at its widest part, of 130 microns. This gigantic vacuole was filled with leucocytes (fig. 39 *c.c*). These were mostly of large size and possessed a very granular cytoplasm, apparently corresponding to Ehrlich's eosinophilic forms, although differing from the highly differentiated varieties of the higher vertebrates. This difference was for the most part in the nuclei which did not assume the typical polymorphous forms. Some of these cells were measured and the following remarkable dimensions were recorded: 7 x 10, 8 x 34, 18 x 78 microns. The posterior extremity of the vacuole was in close relation with one of the large arterial trunks of the stomach-wall.

The zymogen granules in the oxyntic gland cells were everywhere apparent. The animal from which my preparations were made, was evidently fasting, as the granules were diffused through the cytoplasm, as shown by Langley and quoted by Oppel (fig. 29). In my sections, however, the granules seemed to be larger and more condensed at the base of the cell. In one gland I found a leucocyte enclosed within a vacuole (fig. 29 *a*). It contained fragments of undigested matter. Was it a macrophage of Metschnikoff, as described by Ruffer? The vacuole had apparently encroached upon the nucleus of the cell. The picture suggested List's description of the formation of vacuoles by the destruction of epithelial cells by phagocytes.

There has been, from time to time, considerable discussion concerning the stomach glands of Amphibia, which has been participated in by several observers, the point being to determine the homologies between this low primitive form and the higher forms of vertebrate stomach.

As is well known, the stomach in the higher forms is divided into two regions,—the cardiac and pyloric. The two areas possess glands bearing the names of the division of the stomach in which they are found. The cardiac glands are tubular in form, composed of two kinds of cells, the so-called chief and parietal. Of these, the chief cells are pepsin-forming, while the parietal are supposed to furnish the free hydrochloric acid which functions in the process of digestion. The glands of the pyloric

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region have but one kind of cell, which is simple columnar in character.

In the Amphibian stomach, there are no distinctly marked regions. The glands are all of one kind, composed, as stated above, of the clear mucous and smaller granular cells. Some observers have attempted to homologize the granular cells with the parietal forms of the higher vertebrates, while the larger mucous cells are said to represent the chief cells. Langley calls the cardiac glands oxyntic, referring in Amphibia especially to the granular cells. Kingsbury in his researches in Necturus calls these granular cells secreting cells, and, with others, claims that they are responsible for both the pepsin and acid which are found in the stomach fluids.

Some researches by Heidenhain, on the stomach of the higher vertebrates, show that pepsin is formed by both kinds of glands, cardiac and pyloric. The fact that the parietal cells furnish the hydrochloric acid has not yet been fully demonstrated. Whether they do or not, it is certain they do not exist in the Amphibian stomach so far as known. It has been shown by Kingsbury for Necturus, and by Langley for the frog, that the stomach of these animals produces rennin. It is known that this substance is formed by the chief and pyloric cells in the higher forms, the same cells secreting both this substance and pepsin. The mucus secreted in the stomach of forms higher than the Amphibia is the product of the mucous cells lining the gland mouths and the columnar cells of the surface epithelium. This condition does not differ from that in the Amphibia, except in the larger quantity excreted in the latter.

To one who has seen the pyloric gland cells in the higher vertebrate stomach when they are filled with secretion, the resemblance between them and the large clear cells in Amphibia will be very apparent. It is not at all certain that the latter are exclusively mucous cells. It is very possible that they furnish some of the active agents of digestion. May they not prove to be for the Amphibian stomach the same as the pyloric glands for the higher vertebrates, while the secreting cells may be homologous with the chief and perhaps the parietal cells of the cardiac glands?

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INTESTINE.

At the pyloric end of the stomach the muscular layers become very much thickened. This is true especially of the circular layer, suggesting the sphincter at the pylorus in the higher forms. When the intestine is reached, the changes in these layers are very marked. At the point where the stomach becomes diminished in size, just at the entrance of the duodenum, the circular layer becomes very much reduced, while the outer longitudinal layer consists of a single layer of cells. There is a very abrupt change in the epithelium at this point. The ventral fold of the stomach mucosa is projected for a short distance into the intestine, carrying with it its characteristic mucous cells. With this exception the entire character of the epithelial structure is changed.

The surface is covered with two kinds of cells, —columnar and goblet. The former is a striped cell, the stripe covering the free border. The stripe is striated, the striae being parallel to the long axis of the cell. The cells are large, broad at their free ends and tapering to the points of attachment. The nucleus is oval and situated at the inner third of the cell. The cytoplasm has a peculiar reticulated structure, the reticulations having elongated meshes, the long diameter of which corresponds to that of the cell (fig. 33). It does not take the stain as intensely as does that of the cells of the stomach and œsophagus. The goblet cells are much less numerous than the columnar. The thecæ are cup-shaped, and, in many cases, the attached extremity is drawn out into a long thin body giving the cell a very peculiar outline. The nuclei of the epithelial cells are placed at different levels, giving the structure the appearnce of being stratified. This characteristic, however, is not nearly so marked as in the stomach and œsophagus, (figs. 30, 33, 36, and 37).

There is a well-developed muscularis mucosæ, outside of which is a fibrous coat containing the vascular elements. There are two thin layers of muscle,—an inner circular and an outer longitudinal. The contrast between the thickness of the muscle layers in comparison with that of the stomach wall is very striking.

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The mucosa of the duodenum is thrown into a series of tall folds projecting into the lumen, very strikingly suggestive of the valvulæ conniventes of the higher vertebrates. At the bases of the mucous folds, in the submucous coat, occur groups of cells. The cell body is difficult of demonstration owing to the small quantity of cytoplasm. The nuclei are arranged so that they follow a more or less circular outline and they would suggest glandular structures (fig. 43 *b*). Kingsbury, in his studies of Necturus, found these structures and claims to have seen a lumen. In his drawings he presents a figure showing a neck. Bizzozero, in his studies of Proteus, did not see the glands, and, commenting on the work of Paneth on the same form, claims that he mistook supplementary mucous folds for glands. I was unable to demonstrate a lumen in any of my preparations, notwithstanding that all the structures were clearly defined.

THE CLOACA.

The character of the intestinal epithelium does not change materially until it approaches the cloaca. This, too, may be said of the other coats which make up the intestinal wall. At the lower end of the intestine the epithelium becomes modified by the increase in the number of goblet cells. At first this increase is gradual until when the intestine reaches the cloaca the mucous membrane is composed entirely of these cells. This condition continues for some distance, but the goblet cells are gradually replaced by the columnar form which makes up the bulk of the surface cells throughout the body of the cloaca. At the anal end of the cloaca the goblet cells are again most numerous.

Beneath the surface of the cloaca the epithelial cells are disposed in strata. The form and disposition of the cells remind one very strikingly of the transitional stratified epithelium found in the pelvis of the kidney, ureters and bladder of the higher vertebrates.

Under the surface stratified epithelium there occurs a layer of cells which are arranged in groups. These groups at first sight suggest cross-sections of tubular glands. After careful study the writer is of the opinion that they are not glands, but are

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germ centres in which new cells are formed and pushed up to the epithelial surface to take the places of the constantly degenerating surface cells.

This conclusion was reached for the following reasons:—Nowhere among these groups of cells is there to be demonstrated a lumen. Indeed, in a large number of instances, the arrangement of the cells would manifestly make this impossible. In the majority of the groups the cells seem to have no definite arrangement. Here and there within the groups are cells in active division, as demonstrated by the many examples of mitotic figures which are everywhere to be seen. The nuclei are very large, filling the greater part of the cell and occurring in the centre of the cell body. In no case was there any sign of secretion in the cytoplasm of any of the cells, although in the basal strata of the surface epithelium goblet cells filled with mucin were very abundant.

At the anterior and posterior extremities of the region, where the layer in question is most prominent, the goblet cells in the epithelial layer are most numerous. At these points, the mucous or goblet cells are seen in process of formation and may be traced in all stages of development up to the surface layers (fig. 24). In the wall of the cloaca proper the surface epithelium, as above stated, is transitional stratified. This form of epithelium, it will be remembered, lines the urinary bladder, ureters and pelvis of the kidney in the mammals (a fact which is at least interesting considering the origin of the bladder from this primitive organ), and like this tissue, wherever found, the lower layers are germinative (fig. 20). In the tissue under consideration, the cells of the lower layers take their origin from those composing the bodies under discussion, and may be traced, as in the case of the goblet cells, from this point to the surface.

Stannius, in 1856, makes the general statement that these structures are glands, basing his opinion upon observations made by other observers upon several forms of Amphibia. He says "These glands are situated in the circumference of the cloaca and open into it by many ostia." Oppel, in his studies of Proteus, calls them glands and says " They are club-shaped and many of them have two divisions at the lower part" (fig.

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25). Kingsbury, for Necturus, gives very little attention to the cloaca and does not mention these structures at all.

Everywhere throughout the tissue are seen large phagocytic cells, which are clearly identical with the macrophages of Metschnikoff and those described by Ruffer in the tonsils and Peyer's patches of the rabbit (figs. 13, 41). In the presence of so much degenerating cytoplasm in the remnants of the disintegrating mucous cells, is probably to be found the chemotactic attraction which draws them to this point. This will be discussed under the head of Leucocytes.

BILE AND PANCREATIC DUCTS.

For a short distance after its origin from the pylorus, the intestine passes forward toward the anterior end of the stomach. It thus forms a loop, the outer limb of which comes into close relation with the liver and, in this loop, lies the pancreas (fig. 35). This organ is roughly stellate in form (fig. 44) and is so placed that two of its lobes come in contact with the intestine at different points. One point of contact occurs a short distance from the pylorus, while the other is found very near the place where the intestine comes into relation with the liver. The latter lobe of the pancreas comes into actual contact with both the intestine and the liver.

The liver is large, extending from the pericardium anteriorly to the pyloric end of the stomach posteriorly (fig. 1). Its posterior border is throw into a series of small lobes, between two of which the gall bladder is placed. The bile duct on emerging from the gall bladder is, for a short distance, free in the body cavity; after which it enters the lobe of the pancreas, which lies between the liver and intestine. Passing through this lobe of the pancreas it enters the intestine. Four hepatic ducts arise independently in the liver and, passing into the pancreas, unite with the bile duct. Two of these join the bile duct just before it enters the intestine, while the remaining two unite with it within the intestinal wall, just before it enters the lumen. Thus the three tubes may be traced independently into the intestine and enter the lumen by a single mouth. On their way through the pancreas, these ducts are joined by numerous pan-

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creatic ducts. An independent pancreatic duct enters the intestine at the point where the pancreas touches it near the pylorus (fig. 44 *e*).

LEUCOCYTES.

These bodies were found throughout the length of the enteron in the submucous connective tissue, in the epithelium, and even in the cardiac glands. They were of various shapes and sizes, the smaller ones suggesting the lymphocyte, the intermediate sizes reminding one of the highly differentiated polymorphonuclear forms. The very large ones, particularly those found in the walls of the cloaca, suggest the macrophages of Metschnikoff. In some instances these latter cells were of enormous size, as will be seen by some measurements given elsewhere. List has given an account of the leucocytes observed by him in the cloaca of *Raja miraletus*. He shows some remarkable forms assumed by these cells in the process of their invasion by amoeboid movement. Some such forms of nuclei will be seen in fig. 40.

This process is not uncommon in some pathological conditions in the mammals, where nuclei are seen reaching out from one part of the tissue to another by the same process of elongation. According to List the leucocyte invades the cell, surrounds or engulfs the nucleus, and finally destroys the cytoplasm by absorption. By this process a vacuole is formed around the invading leucocyte, which may occupy the place in the tissue formerly occupied by one or more cells. Sometimes only a portion of the cytoplasm is destroyed, and the nucleus is not invaded. In this case the vacuole would appear in the cytoplasm of the cell; in other instances the leucocyte has found its way between the cells in the cement substance, and a part of the cytoplasm of two adjacent cells has been destroyed to form the vacuole (fig. 30 *a*, *b*, *c*, and fig. 34 *b*, *c*).

The reason for their presence in the epithelium seems to be the question awaiting answer. Every histologist knows how constantly these organisms are met with in the tissue of the higher forms. Some late researches of Brinckerhoff and Tyzzer, on the leucocytes found in the rabbit would seem to confirm the

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conclusions of Ehrlich, that the migration of these cells is due to chemical affinity existing in their molecular composition which acts when they come into relation with the substances in the body that answer to, or satisfy the group of atoms possessing the special attractive stimulus. This establishes the principle of chemotaxis as the attractive agent which accounts for their presence everywhere in the body. In the case of the polymorphonuclear leucocyte, it is the bacterial toxins which serve as the attractive stimuli.

Ruffer, in his investigations on the phagocytic forms in the tonsil and Peyer's patches of the rabbit, shows that there are certain gigantic organisms present which have devoured the ordinary leucocyte (figs. 2 *c*, 30 *a* and 34 *b*). These cells he calls, after Metschnikoff, macrophages. Councilman, Mallory and Pearce have shown that these cells are of endothelial origin, and are differentiated endothelial cells. It has also been shown that the chemotactic attraction for these cells is degenerating cell substance, whether nuclear or cytoplasmic.

It seems to the writer that these facts adequately account for the presence of these cells in the tissues of the enteron. This is true not only for the microphages, or ordinary leucocytes, but also for the macrophages, or large mononuclear forms as well. Not only this, but the devouring of one by the other, so frequently observed, is accounted for.

The habitat and mode of life of Amphibia would render them specially liable to invasion by bacterial forms which would thus naturally be found most abundantly in the enteron. Here their absorption would bring them immediately into the epithelial layer, forming the specific chemotactic attractive element for the leucocyte. This condition would be especially marked in the cloaca, where the rejecta of the body is stored. Here the leucocytes would become loaded with toxins to the extent that degenerative processes would be established in their cytoplasm, rendering them a menace to the body and making them the legitimate prey to the phagocytic macrophage.

In the cloaca the tissue offers a particularly fertile field for these cells on account of the great amount of degenerating cyto-

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plasm here present, as a result of the disintegrating goblet cells which are destroyed in the process of their own activities.

Kingsbury, in his studies of Necturus, offers the conjecture that the leucocytes are in the stomach surface cells, because of the presence of absorbed fat. This would seem impossible from the fact of the improbability of the presence of fat in the stomach epithelium as stated elsewhere.

ABSORPTION OF FAT BY THE STOMACH CELLS.

Kingsbury, in his investigations on Necturus, claims to have found fat in the cytoplasm of the cells of the stomach epithelium. In his figure of these cells he shows certain granular bodies, which he labels fat. This statement at once raises the question of absorption of fat by the stomach epithelium from the stomach contents.

Oppel mentions certain granular bodies in the epithelial cells of the stomach of Proteus, but passes the subject with the statement that they react feebly to osmic acid. Langley found what he took to be fat in the stomach glands of the frog. In the latter case, the fat, if such it was, could not possibly have been absorbed from the stomach contents, as the secretions are all moving in the opposite direction. Whatever substance is contained in the gland cell, must necessarily have been absorbed from the lymph.

Fat must be acted upon by the pancreatic juice and bile before it can be absorbed, and this, for obvious reasons, is impossible in the stomach. The mere fact that a substance reacts to osmic acid is no adequate proof that it is fat, except under certain definite conditions. Foster mentions certain substances in leucocytes which react in this way, and yet were shown not to be fat.

The granular bodies mentioned for Necturus were also found in Amblystoma, but were interpreted as the granules of forming mucus, which is produced so abundantly by these cells. This conclusion was reached from the following facts : — In the cytoplasm of certain cells were found granules massed together between the nucleus and the free border. At the inner margin these masses possess a clearly defined outline. From the ends

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of these cells plugs of mucus were seen protruding, which seemed to be continuations of the masses within the cell body. Between the area of granules and the nucleus appeared a space comparatively free from granular bodies, where the characteristic structure of the cytoplasm could be seen. A study of figs. 14 and 31 *a*, *b*, *c*, will demonstrate these observations very clearly.

In some cells the masses seemed to be in process of formation. Here several small collections of granules appeared to be merging to form the main body of the structure. In others, they were joined together, and presented an outline which suggested the theca of a goblet cell. In cells where these masses did not occur, the granules were diffused through the cytoplasm, mostly between the nucleus and the free end of the cell. These granules assumed a brownish color under the influence of osmic acid.

SUMMARY.

The mouth cavity is lined by stratified epithelium, thinner on the palate and dorsum of the tongue than elsewhere. Except in these regions, where the cells are low, cubical, and non-ciliate, the lining cells are of the ciliated columnar and goblet type.

Glands penetrate the tongue from the dorsal surface; these are most numerous and longest in the middle and anterior portions. At the base of the tongue they are composed of clear mucous cells; farther forward the deeper ends consist of true secreting cells with large (zymogen?) granules in the free ends.

Some cases of blood capillaries in the epithelium were seen.

Amblystoma differs from Necturus, Proteus, and Triton in the presence of cilia in the mouth and of tubular glands in the tongue.

The mucosa of the œsophagus is thrown into longitudinal folds, covered with ciliated epithelium and fewer goblet cells; no muscularis mucosæ was found.

Although present in the young, glands are absent from the œsophagus of the adult, with the exception of a circle, apparently common to all Amphibia, around the gastric end.

The mucosa of the stomach is folded longitudinally, the folds

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less evident at the pylorus, but the ventral fold continuing into the duodenum. The submucosa and the muscularis mucosæ are present, as is, apparently, the pyloric sphincter.

The stomach is lined by the columnar mucous cells peculiar to the Amphibia. It lacks the differentiated regions of the higher Vertebrata. The tubular glands have clear cells at the neck, granular cells in the deeper portions. The granules are regarded not as fat, but as stages in the formation of mucus. Chief and parietal cells are not distinguished.

The intestine is lined with striped columnar and goblet cells, the former most numerous in the upper and middle regions. The gastric fold in the beginning of the duodenum bears mucous cells like those of the stomach, while goblet cells compose the entire lining at the entrance into the cloaca.

The duodenum has folds recalling the valvulæ conniventes of the higher Vertebrates; at their base groups of cells are so arranged as to recall glands.

The muscular layers of the intestine, particularly the longitudinal layer, are poorly developed at the anterior end.

The epithelium at the beginning of the cloaca is composed entirely of goblet cells, these being gradually replaced by a transitional stratified epithelium with columnar-like cells on the free surface.

Below the surface epithelium of the cloaca are cell aggregates with abundant mitoses. These are regarded as germinal centres for the replacement of the degenerating cells of the surface.

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DESCRIPTION OF FIGURES

The drawings in most cases were made in outline under a 1-8 dry and a 1-10 oil immersion lenses with the camera lucida, and finished subsequently.

Figure 1. Outline drawing of adult animal showing the enteron and its relation to the liver: *a*, pericardium; *b*, liver;

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c, stomach; *d*, duodenum; *e*, intestine; *f*, cloacal end of the intestine; *g*, cloaca; *h*, anal extremity of cloaca; *i*, anus.

Figure 2. Section of epithelial surface of the mouth. *a*, epithelium of the surface showing the columnar ciliated form of the cells. *b*, Mucous cells showing the mucus masses, giving the cell contents a reticulated appearance. *c*, Large macrophage contained in a vacuole. Two are contained in the vacuole, and are, apparently, being devoured by the larger cell. Another of similar nature may be seen at *f*. *d*, Nuclei of underlying cells. *e*, Blood-vessel within the epithelial layer; a larger one may be seen further to the left.

Figure 3. Surface of the mouth with gland-like depressions at *a*. It will be seen that the cells are ciliated.

Figure 3*a*. More highly magnified portion of the foregoing, showing the non-ciliated striped form of cells in the lower portion of the depression.

Figure 4. Section of tongue showing arrangement of gland tubes. *a*, Surface epithelium. *b*, Glands dipping down from the surface. *c*, Muscular fibres in the body of the tongue.

Figure 4*a*. Transverse section of a gland tube, at the anterior extremity of the tongue. *a* is placed in the lumen. Attention is called to the large granules in the lumen end of the cell.

Figure 5. Section of gland tube at the base of the tongue. *a*, The neck of the gland. *b*, Branching of the lumen to form the sacculated structure. *c*, Body of the gland showing massing of cells. *d*, Group of goblet cells.

Figure 6. Surface of the tongue. *a*, Side of the tongue showing the large ciliated cells. *b*, Dorsal surface of the tongue with low polygonal cells without cilia. *c*, Blood vessel in submucous connective tissue.

Figure 7. Epithelium at the stomach end of the œsophagus. *a*, Ciliated and non-ciliated cells. *b*, Stomach cells with plugs of mucus at their free ends.

Figure 8. Ciliated cells of epithelium of œsophagus.

Figure 9. *a*, Surface epithelium of the mouth cavity, showing cilia and stripe. *b*, Leucocytes embedded in cell-cytoplasm. *c*, Large leucocyte containing smaller form enclosed

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in a vacuole. Other leucocytes are seen in various parts of the tissue.

Figure 10. Goblet cells found in the mouths of the gland tubules. At *a* and *c* the nucleus is pushed to the base of the cell. At *b* the nucleus is still free in the cytoplasm.

Figure 11. Section of the tongue farther forward, showing at *d* penetration of glands through the substance of the tongue. Lettering as in fig. 4.

Figure 12. Isolated cells of surface epithelium of mouth cavity. *a*, Ciliated striped cells of the surface. *b*, Polygonal cells of lower and intermediate layers.

Figure 13. Large macrophage which has evidently devoured a cell. *a*, Nucleus of engulfed cell, *b*, Nucleus of macrophage, *c*, Undigested matter, probably fragments of cell cytoplasm in the substance of devouring cell. *d*, Yellow granules.

Figure 14. Cells of the stomach surface epithelium showing mucous plugs extending into the cytophlasm of the cells.

Figure 15. Single gland tube more highly magnified. *a*, Large clear mucous cells. *b*, Lumen. Attention is called to the goblet-shaped cells in the structure.

Figure 16. Goblet cells and leucocytes of mouth epithelium. *a*, Goblet cells. *b*, Leucocytes enclosed in vacuoles.

Figure 17. Large peculiar shaped cells at side of the tongue and angles of the mouth. *a*, This cell shows the impression made in its cytoplasm by pressure from ajacent cells. *b*, Shows how the cells are massed together.

Figure 18. Germinal centre in cloaca. *a*, Germinal centre. *b*, Macrophage with yellow granules. *c*, Mucous cells on their way to the surface. *d*, Cell in mitosis.

Figure 19. Epithelium of the œsophagus. *a*, Ciliated cells. In the depressions will be seen the spindle-shaped cells. *b*, Goblet cells with mucus protruding from them. *c*, Curved cell at the angle of a fold.

Figure 20. Section of epithelial layer of cloaca. *a*, Germinal centre. *b*, Cells moving to the surface. *c*, Surface cells. *d*, Macrophage which has already devoured two microphages like that shown at *e*. Attention is called to the similarity between

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these structures and the transitional stratified epithelium in the urinary tract of the higher vertebrates.

Figure 22. Section to show the peculiar elongated surface cells in the epithelium of the cloaca. *a*, is placed on a goblet cell. *b*, Goblet cells in process of development. *c*, Germinal centre. *d*, Submucous coat. *e*, Cells on the way to the surface to be formed into goblet cells. The surface cells are all goblet cells.

Figure 23. Peculiar shaped cells in the gland mouths of stomach.

Figure 24. Section of epithelial wall of cloaca. *a*, Germinal centre. *b*, Goblet cells. *c* is placed in the space made vacant by a degenerated goblet cell. *d*, Leucocyte in epithelial cell. *e*, Same, in germinal layer. *f*, Submucous connective tissue. *g*, Macrophage.

Figure 25. Section of epithelial surface and underlying structure in the circumference of the cloaca. *a*, Centre of germinal layer. *b*, Cells moving to the surface. *c*, Goblet cells in process of development. *d*, Nuclei of surface cells. *e*, Goblet cell reversed. *f*, Connective tissue of submucous coat.

Figure 26. Isolated mucous cells from the cloaca at *a*. At *b*, mucous cells from the human cæcum to show comparative size.

Figure 27. Junction of œsophagus and stomach, showing beginning of stomach glands. *a*, Œsophageal epithelium. *b*, Stomach epithelium. *c*, Mucous gland of œsophagus with large clear cells. *c′* Stomach gland, showing large clear mucous cells at the neck and granular secreting cells in the gland tube.

Figure 28. Section of stomach mucosa, showing surface epithelium and stomach glands. *a*, Gland mouth. *b*, Clear cells at the neck of gastric gland. *c*, Secreting cells, forming gland tubules.

Figure 29. Transverse sections of gland tubules. The granules are diffuse, but show a tendency to gather at the basal side of the cell. At *a* will be seen a large leucocyte within a vacuole. The vacuole has encroached upon the cell nucleus.

Figure 30. Surface epithelium of intestine showing leucocytes. *a*, A large phagocytic form, seemingly in the act of devouring smaller forms. *b*, A leucocyte escaping in the intes-

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tinal lumen. *c*, A number of surface intestinal cells showing various forms of leucocytes is cytoplasm.

Figure 31. Snrface cells of stomach epithelium showing the mucous masses in the cells in the process of formation. *a*, Ordinary mucous cell, the granules being diffused evenly through the cytoplasm. At *b* the granules have massed together. *c* shows the masses forming separately and merging.

Figure 32. Macrophages from the human cæcum. The granules are yellow and are composed of blood coloring matter.

Figure 33. Section of the summit of an intestinal fold. *a* is placed in the centre of an epithelial cell. The cytoplasm shows the elongated reticular structure. The cell bears a stripe which is striated. *b* shows the connective tissue of the submucous layer. The letter is placed beside a blood vessel. At *c* are seen the cells at the side of the folds.

Figure 34. A group of cells from the epithelial surface of the cloaca. *a*, Surface cell containing two leucocytes. *b*, A group of small leucocytes which have evidently destroyed a part of the cell nucleus at *c*. *d*, A goblet cell with its characteristic reticulated cytoplasm.

Figure 35. This figure shows the stomach, *a*; the loop formed by the recurving duodenum, *b*; and the pancreas occupying the the loop. At *c* the pancreas comes into contact with the duodenum, and again at a point just posterior to the pylorus. The liver is shown turned back to expose the pancreas.

Figure 36. Sections to show particularly long cells of the intestinal epithelium. *a* is placed in the theca of a goblet cell. Attention is called to its peculiar shape. *b*, An ordinary surface cell. *c*, A typical goblet cell.

Figure 37. Section of depression between the intestinal folds to show the curving of the cells to accommodate them to their position.

Figure 38. Microphages from the cloaca. These cells are evidently in process of development. The nuclei in the group at *a* show evidence of transformation.

Figure 39. Macrophages *a* and *c* show apparently amœboid movement. *b* shows nucleus suggestive of the polymorphous

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forms of higher vertebrates. *d*, Two macrophages from a human lymph node.

Figure 40. Germinal centre in cloaca. *a*, Peculiar elongated nuclei, suggesting those shown by List in the cloaca of *Raja miraletus*. *b*, Macrophage. In the group will be seen a cell in mitosis.

Figure 41. This figure shows an isolated macrophage.

Figure 42. Cell in mitosis from a germinal centre in the cloaca.

Figure 43. Section showing a so-called intestinal gland. *a*, Surface cells. *b*, Centre of gland. *c*, Leucocytes in vacuoles in the epithelial cells.

Figure 44. The duodenum turned over to expose the form of the pancreas. *a*, Stomach. *b*, Duodenum. *c*, Pancreas. *d*, Gall, bladder. *e*, Point where the pancreas touches the duodenum and where the independent pancreatic duct enters. Between the gall bladder and duodenum is seen a lobe of the pancreas. Through this lobe the bile duct enters the intestine.

Figure 45. Junction of œsophagus and stomach, showing mucous gland. *a*, Ciliated epithelium of œsophagus. *b*, Stomach surface epithelium with mucous cells. *c*, Large clear cells of mucous gland. *d*, Submucous coat.

NOTE.—Figures 32, 38 and 39 are grouped for a comparative study of microphages and macrophages in the process of development and amœboid movement. At *a* will be seen a group of microphages in which the nuclei show evidences of transformation. At *b* the nucleus is suggestive of that in the polymorphous forms of the higher vertebrates. At *c*, fig. 39, are shown cells which have assumed forms suggesting amœboid movement. At *d* are two cells from a human lymph node, the one to the right unpigmented, the other containing pigmented granules consisting of blood-coloring matter. Fig. 32 shows a group of macrophages from the human cæcum, highly pigmented with yellow granules. The general shape of these cells suggests their endothelial origin.

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CATALOGUE OF THE MAMMALS IN THE BARNUM MUSEUM OF TUFTS COLLEGE.

By A. E. Preble.

The collections of the Barnum Museum consist in great part of material derived from two sources: First, a collection purchased by Mr. P. T. Barnum from H. A. Ward of Rochester, N. Y., and presented by him to the College; and second, of various animals which have died in the Barnum-Bailey Menagerie, and which have been given to us. These have been mounted by various taxidermists, chiefly, however, by Ward's establishment.

MONOTREMATA.

Ornithorhynchus anatinus, Duck-billed Platypus	Victoria, Australia
Echidna setosa, Silky-haired Echidna	Tasmania
Echidna hystrix, Spiny Echidna	Victoria, Australia

MARSUPIALIA.

Didelphys virginianus, Oppossum	Virginia
Phalcolomys wombat, Wombat	Victoria, Australia
Phascolarctos cinereus, Koala	Victoria, Australia
Phalanger orientalis, Gray Cuscus	Duke of York Island
Acrobata pygmæa, Pigmy Phalanger	New South Wales
Trichosurus vulpecula, Vulpine Phalanger	Victoria, Australia
Petaurista taguanoides, Flying Phalanger	New South Wales
Belideus sciurus, Squirrel Flying Phalanger	Australia
Perameles lagotis, Rabbit-eared Perameles	New South Wales
Perameles gunni, Gunn's bandicoot	Australia
Macropus giganteus, Giant Kangaroo	Australia
Macropus giganteus, " " skeleton	New South Wales
Macropus rufus, Red Kangaroo	Australia
Macropus rufus " "	No locality
Halmaturus ruficollis, Wallaby	Victoria, Australia
Halmaturus ualabatus, Black-tailed Wallaby	Australia

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Halmaturus thetidis, Small Wallaby	Australia
Hypsiprymnus murinus, Rat Kangaroo	New South Wales
Petrogale penicillata, Brush-tailed Rock Kangaroo	New South Wales
Dasyurus viverrinus, Native Dasyure	New South Wales
Dasyurus maculatus, Dasyure	Australia

EDENTATA.

Tatusia novemcincta, Peba Armadillo	Demerara
Chlamydophorus	No Locality
Cholœpus didactylus, Two-toed Sloth	Brazil
Cholœpus hoffmanni, Hoffmann's Sloth	Costa Rica
Myrmecophaga jubata, Great Anteater	Brazil
Orycteropus æthiopicus, Orycterope, Aard Vark	South Africa
Manis javanica, Pangolin	Malay Peninsula
Manis indicus, Scaly Pangolin	Malay Peninsula

RODENTIA.

Lepus campestris, White-tailed Jackrabbit	Nebraska
Lepus arcticus, Arctic Hare	Sweden
Lagomys princeps, Pika	Colorado
Hydrochœrus capybara, Capybara	Orinoco River
Cavia australis, Southern Cavy	Argentine Republic
Cœlogenys paca, Paca	South America
Hystrix cristata, African Porcupine	Africa
Hystrix cristata " "	North Africa
Hystrix cristata, Skeleton "	North Africa
Cercolabes prehensilis, Tree Porcupine	Brazil
Erethizon dorsatum, Canadian Porcupine	Maine
Capromys pilorides, Coypu	Cuba
Dipus ægypticus, Gerboa	North Africa
Geomys bursarius, Pouched gopher	Michigan
Spalax typhlus, Mole Rat	Asia Minor
Fiber zibethicus, Muskrat	New York State
Myodes lemmus, Lemming	Germany
Microtus pennsylvanicus, Meadow Vole	New York State
Mus decumanus, Common Brown Rat	New York State
Mus rufescens, Tree Rat	South India

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Peromyscus leucopus, White-footed Mouse	United States
Neotoma cinerea, Mountain Wood Rat	Wyoming
Castor fiber, American Beaver	Nebraska
Haplodon leporina, Sewellel	Oregon
Arctomys monax, Woodchuck	New York State
Cynomys ludovicianus, Prairie Dog	Kansas
Spermophilus graminurus, Ground Squirrel	
Spermophilus citillus, Souslik	Russia
Tamias sp?	Western States
Sciurus ludovicianus, Fox Squirrel	Texas
Sciurus bicolor, Indian Squirrel	Singapore
Sciurus vulgaris, European Squirrel	France
Sciurus plantani, Cocoa Squirrel	Salangore
Sciuropterus sabrinus macrotis, Flying Squirrel	New York State
Pteromys nitidus	Borneo

INSECTIVORA.

Ericulus setosus, Tendrec	Madagascar
Tupaia (species unknown), Squirrel Shrew	Borneo
Macroscelides intufi, Elephant Shrew	Madagascar
Erinaceus europeus, European Hedgehog	Europe
Blarina brevicauda, Short-tailed Shrew	College Hill, Mass.
Blarina brevicauda, Skeleton	College Hill, Mass.
Myogale moschata, Desman	Russia
Scalops aquaticus, American Mole	California
Talpa europea, European Mole	France
Galeopithecus philippinensis	Philippine Islands

CHIROPTERA.

Pteropus melanopogan	New Britain I.
Pteropus edwardsii, Flying Fox	Ceylon
Pteropus edwardsii, skeleton	East Indies
Cynopterus marginatus	China
Vespertilio bicolor	
Rhinolophus hipposiderus	Europe
Cheiromeles torquatus	Borneo
Harpyia major	Duke of York Island

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Eomycteris spelea	Malay Peninsula
Melanycteris melanops	Duke of York Island

CETACEA.

Phocæna communis, Atlantic Porpoise	Coast of New York
Delphinaterus catodon, Cast of head, White Whale	
Globiocephalus melas, Cast of head, Blackfish	
Grampus griseus, Cast of whole animal, Cowfish	
Grampus griseus, Cast of head	

SIRENIA

Manatus americanus, Manatee	Demerara

HYRACOIDEA.

Dendrohyrax dorsalis, African Coney	West Africa

PROBOSCIDEA.

Elephas indicus, "Jumbo"

UNGULATA.

Tapirus terrestris, American Tapir	South America
Tapirus indicus, Malayan Tapir, skeleton	Malay Islands
Atelodus bicornis, Two-horned Rhinoceros	South Africa
Atelodus bicornis, skeleton	South Africa
Equus burchelli, Burchell's Zebra	South Africa
Equus caballus, skeleton	
Sus scrofa, Wild Boar	France
Dicotyles torquatus, Collared Peccary	Mexico
Dicotyles torquatus, " "	Texas
Camelus dromedarius, Dromedary, young	Bridgeport, Conn.
Camelus dromedarius, Dromedary	North Africa
Lama huanaco, huanaco	Peru
Lama huanaco, skeleton	
Lama vicugna, viçuna	Bolivia
Lama " "	South America
Tragulus javanicus, Javanese Chevrotain	Java
Cervus canadensis, American Elk	North America
Cervus canadensis, skeleton	North America

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Axis maculatus, Axis Deer	S. W. India
Alces americanus, Eastern Moose	Maine
Capreolus, (species not determined) Roedeer	
Rangifer tarandus, Reindeer	
Capreolus capræa, European Roedeer	Turkey
Giraffa camelopardalis, Giraffe	Africa
Bison americanus, American Bison	North Platte, Neb.
Bibos indicus, Zebu	India
Antilope cervicapra, Black Buck	India
Oreas canna, Eland	South Africa
Oreas canna, skeleton	South Africa
Portax pictus, Nilgau	India
Portax pictus, Nilgau, skeleton	India
Oryx beisa, Oryx	No locality
Oryx beisa, Oryx, skeleton	
Gazella dorcas, Gazelle	Nubia
Antidorcas euchore, Springbok	Africa
Alcelaphus caama, Hartebeest	South Africa
Alcelaphus caama "	South Africa
Alcelaphus caama, skeleton	South Africa
Cannochaetes gnu, White tailed Gnu	South Africa
Rupicapra rupicapra, Chamois	Italy
Oreamnos montanus, Rocky Mountain Goat	N. W. Territory
Ovis montana, Rocky Mountain Sheep	Montana
Ovis tragelaphus, Maned Sheep	Atlas Mts.

CARNIVORA.

Procyon lotor, Raccoon	Cambridge
Procyon lotor, Raccoon	New York
Nasua rufa, Coati	Brazil
Nasua rufa, skeleton	
Cercoleptes caudivolvulus, Kinkajou	Mexico
Helarctos euryspilus, Bornean Sun Bear	Borneo
Ursus americanus, Black Bear	No Locality
Ursus horribilis, Grizzly Bear	Utah
Thalarctos maritimus, Polar Bear	Greenland
Thalarctos maritimus, skeleton	Greenland
Lutra canadensis, American Otter	Nebraska

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Ictonyx capensis, Zorilla	Natal, S. Africa
Mephitis fœtida, Eastern Skunk	New York State
Meles taxus, European Badger	Germany
Gulo luscus, Wolverine	Northern States
Lutreola vison, Mink	N. America
Mustela americana, American Sable	Montana
Mustela sibirica, (Sable)	Pekin
Vulpes fulvus, Red Fox	Oregon
Canis lupus, European Wolf	Sweden
Canis aureus, Jackal	Ceylon
Nyctereutes procyonoides, Raccoon Dog	Japan
Hyæna striata, Striped Hyæna	India
Hyæna striata, Skeleton	W. Africa
Viverra malaccensis, Lesser Indian Civet	Malacca
Viverra zibetha, Indian Civet Ninopo,	China
Paradoxurus (species undetermined), Palm Civet	India
Cynogale bennetti, Palm Civet	North Borneo
Herpestes madagascarensis, Malagassy Mongoose	Madagascar
Felis tigris, Tiger	
Felis tigris, Tiger skeleton	
Felis leo, Lion, male	Africa
Felis concolor, Puma	
Felis concolor, Puma, skeleton	Texas
Felis chaus, Chaus	India
Felis pardus, Leopard	S. W. India
Felis pardus, African Leopard	Africa
Felis leo, Lion, female	Africa
Felis leo, Lion, male, skeleton	Africa
Lynx rufus, American Wild Cat	Nebraska
Lynx rufus, American Wild Cat, Skeleton	Maine
Otaria ursina, Northern Fur Seal, bachelor	Alaska
Otaria ursina, Northern Fur Seal, pup	Alaska
Eumetopias stelleri, Californian Sea Lion	California
Phoca grœnlandica, Harp Seal	Greenland
Phoca vitulina, Harbor Seal	Coast of New York
Phoca vitulina, Harbor Seal	New England
Phoca vitulina, Skeleton	New York State

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PRIMATES

Vavecia varia, Ruffled Lemur	Madagascar
Nycticebus tardigradus, Slow Lemur	Madagascar
Jacchus œdipus, Pinche	Guiana
Midas ursulus, Tamarin	Brazil
Callithrix nigrifrons	Brazil
Pithecia monachus, Monk Cebus	S. America
Chlorocebus cynosurus,	S. America
Chlorocebus cynosurus, Skeleton	S. America
Mycetes seniculus, Golden Howler	Demerara
Ateles bartletti, Spider Monkey	Darayacu
Cyhanoceplus porcarius, Chacma	Africa
Cynocephalus babuin, Baboon	Africa
Cynocephalus babuin, Baboon	West Africa
Cynocephalus babuin, Skeleton	
Cynocephalus babuin, Skeleton	West Africa
Cynocephalus babuin	West Africa
Cynocephalus mormon, Mandrill	
Macacus rhesus, Bunder, Skeleton	S. America
Macacus nemestrinus, Bruk	Lading, Borneo
Hylobates leuciscus, Gibbon	North Borneo
Simia satyrus, Orang-utan	N. Borneo
Anthropopithecus troglodytes, Chimpanzee, Skeleton	Africa

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